

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

DETERMINANTS OF BUTTERFLY DISTRIBUTION  
IN THE AMAZONIAN FOREST

RAFAEL MAGALHÃES RABELO

Manaus, Amazonas

Janeiro, 2022

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IN THE AMAZONIAN FOREST

Orientador: WILLIAM ERNST MAGNUSSON

Tese apresentada ao Instituto Nacional  
de Pesquisas da Amazônia como parte  
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MINISTÉRIO DA  
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### PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

#### ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA.

Aos 21 dias do mês de Janeiro do ano de 2022, às 09h30min, por videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o **Dr. Jessie Pereira dos Santos**, da Universidade Estadual de Campinas – UNICAMP, a **Dra. Gabriela de Paula Souza Zuquim**, da Universidade de Turku, o **Dr. Fabricio Beggiato Baccaro**, da Universidade Federal do Amazonas – UFAM, a **Dra. Camila Cherem Ribas**, do Instituto Nacional de Pesquisas da Amazônia – INPA e o **Dr. Geraldo de Brito Freire Junior**, da Universidade de Nevada. Tendo como suplentes o Dr. Pedro Aurélio Costa Lima Pequeno, do Instituto Nacional de Pesquisas da Amazônia – INPA, e a Dra. Fernanda de Pinho Werneck, do Instituto Nacional de Pesquisas da Amazônia – INPA sob a presidência Dr. William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia – INPA, a fim de proceder a arguição pública do trabalho de **TESE DE DOUTORADO de RAFAEL MAGALHÃES RABELO**, intitulada: **"DETERMINANTS OF BUTTERFLY DISTRIBUTION IN THE AMAZONIAN FOREST"**, orientado pelo Dr. William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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DRA. GABRIELA DE PAULA SOUZA ZUQUIM

DR. FABRICIO BEGGIATO BACCARO

DRA. CAMILA CHEREM RIBAS

DR. GERALDO DE BRITO FREIRE JUNIOR

DR. PEDRO AURÉLIO COSTA LIMA PEQUENO

DRA. FERNANDA DE PINHO WERNECK

*[Handwritten signatures of the examiners]*

*[Handwritten signature of the coordinator]*  
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### Sinopse

Estudou-se o efeito de fatores históricos e ecológicos na distribuição de *Antirrhea ulei*, uma borboleta endêmica do Pantepui. Avaliou-se os efeitos dos gradientes ambientais entre florestas de várzea e terra firme na distribuição de borboletas na Amazônia Central. Avaliou-se a influência dos filtros ambientais e de dispersão na riqueza e composição de espécies, quantificando a importância relativa desses fatores.

**Palavras-Chave:** macroecologia, distribuição, borboletas, filtragem ambiental, limitação de dispersão.

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*"It is in the height of the dry season that the greatest number and variety of butterflies are found in the woods; especially when a shower falls at intervals of a few days. An infinite number of curious and rare species may then be taken, most diversified in habits, mode of flight, colours, and markings...*

*But no description can convey an adequate notion of the beauty and diversity in form and colour of this class of insects in the neighbourhood of Ega. I paid especial attention to them, having found that this tribe was better adapted than almost any other group of animals or plants, to furnish facts in illustration of the modifications which all species undergo in nature under changed local conditions."*

— Henry Walter Bates, *The Naturalist on the River Amazons*.

## Resumo

### Determinantes da distribuição de borboletas na floresta Amazônica

A distribuição das espécies é influenciada por processos históricos, ecológicos e evolutivos, sendo determinada por filtros de dispersão, ambientais e bióticos. Estes filtros atuam em diferentes escalas espaciais para selecionar a composição de espécies local. Os objetivos desse trabalho foram: (i) avaliar como as mudanças históricas no padrão de distribuição de *Antirrhea ulei* – uma borboleta rara e endêmica do Pantepui – foram influenciadas pelas flutuações climáticas desde o último máximo glacial (LGM; ~21.000 anos atrás); (ii) testar se abundância, riqueza e composição de espécies difere entre florestas de várzea e terra firme na Amazônia Central, avaliando o papel da inundação das florestas na estrutura da assembleia em escalas locais; e (iii) avaliar a influência da limitação de dispersão e da filtragem ambiental como determinantes da distribuição das espécies em amplas escalas na Amazônia. A distribuição de *A. ulei* foi fortemente influenciada por gradientes ambientais. As projeções históricas de sua distribuição sugerem que a espécie provavelmente possuía uma área de ocupação mais ampla durante o LGM, tendo migrado para alto dos tepuis atuais assim que seu habitat adequado foi sendo perdido durante o aquecimento do Holoceno. Esses resultados estão de acordo com a Hipótese de Migração por Vicariância e ajudam a entender a evolução da biota do Pantepui. As florestas de várzea apresentaram maior abundância e densidade de espécies, provavelmente devido a alta produtividade primária dessas florestas. Além disso, Foi encontrada uma diferença pronunciada na composição de espécies entre várzea e terra firme, e a substituição de espécies foi fortemente associada às mudanças ambientais e bióticas entre esses tipos florestais. Esses achados reforçam o papel da inundação de florestas alagáveis da Amazônia como um importante filtro ambiental atuando em escalas locais. Em escalas mais amplas, a forte substituição de espécies ao longo de gradientes ambientais, especialmente climáticos, sugere que as espécies são especializadas em diferentes partes dos gradientes ambientais, particionando seus nichos para permitir a coexistência. Os efeitos da distância, posição e barreiras geográficas tenderam a ser menos importantes, sugerindo que as borboletas são menos prováveis de serem limitadas por dispersão. Esses resultados sugerem que as limitações ambientais são mais importantes que a limitação de dispersão (isolamento por distância ou barreiras geográficas) para explicar a distribuição de borboletas Amazônicas em amplas escalas.

## Abstract

### Determinants of butterfly distribution in the Amazonian forest

Species distribution is driven by historical, ecological and evolutionary processes, being determined by dispersion, environmental and biotic filters. These filters act at different spatial scales to select local species composition. The aims of this work were: (i) to assess how historical changes in the distribution of *Antirrhea ulei* – a rare butterfly endemics to the Pantepui – were influenced by climatic fluctuations since the last glacial maximum (LGM; ~21,000 years ago); (ii) test whether the abundance, richness and composition of butterfly species differ between *várzea* and *terra firme* forests in Central Amazonia, evaluating the role of forest flooding in assemblage structure at local scales; and (iii) evaluate the influence of dispersion limitation and environmental filtering as determinants of species spatial distribution at large scales in the Amazon. The distribution of *A. ulei* was strongly influenced by environmental gradients. Historical projections of its distribution suggest that the species likely had a wider area of occupancy during the LGM, migrating upwards to the present-day tepuis as its suitable habitat were being lost during Holocene warming. These results are in accordance with the Vicariance-Migration Hypothesis and help to understand the evolution of the Pantepui biota. The *várzea* forests showed greater abundance and density of species, probably due to the high primary productivity of these forests. Also, a pronounced difference in species composition was found between *várzea* and *terra firme*, and species turnover was strongly associated to environmental and biotic changes between these forest types. These findings reinforce the role of the flooding as an important environmental filter acting at local scales in the Amazonian floodplain forests. At larger scales, the strong species turnover along environmental gradients, especially climatic, suggests that species are specialized in different parts of the environmental gradients, partitioning their niches to allow for coexistence. The effects of distance, position and geographic barriers tended to be less important, suggesting that butterflies are less likely to be limited by dispersal filters. Thus, these results suggest that environmental constraints are more important than dispersion limitation (isolation by distance or geographic barriers) to explain the distribution of Amazonian butterflies at large scales.

## Sumário

|   |           |
|---|-----------|
| <b>Lista de Figuras.....</b>  | <b>ix</b> |
| <b>Introdução geral.....</b>  | <b>1</b>  |
| <b>Objetivos.....</b>   | <b>4</b>  |
| <b>Capítulo I. – Finding a lost species in the “Lost World”: predicted habitat occupancy by an endemic butterfly in a Neotropical sky-island archipelago.....</b> | <b>5</b>  |
| <b>Capítulo II. – The role of river flooding as an environmental filter for Amazonian butterfly assemblages.....</b>  | <b>13</b> |
| <b>Capítulo III. – The relative role of environment and dispersal as drivers of Amazonian fruit-feeding-butterfly distributions.....</b>                          | <b>15</b> |
| <b>Síntese.....</b>   | <b>40</b> |
| <b>Referências bibliográficas.....</b>  | <b>42</b> |
| <b>APÊNDICE A - MATERIAL SUPLEMENTAR DO ARTIGO PUBLICADO EM <i>Insect Conservation and Diversity</i> (Capítulo I).....</b>  | <b>45</b> |
| <b>APÊNDICE B - MATERIAL SUPLEMENTAR DO ARTIGO PUBLICADO EM <i>Frontiers in Ecology and Evolution</i> (Capítulo II).....</b>                                      | <b>52</b> |
| <b>APÊNDICE C - MATERIAL SUPLEMENTAR DO MANUSCRITO EM PREPARAÇÃO PARA <i>Ecography</i> (Capítulo III).....</b>  | <b>63</b> |

## Lista de Figuras

### Capítulo I.

**Figure 1.** Dorsal (a) and ventral (b) view of a male specimen of *Antirrhea ulei* collected at Uei Tepui, Roraima State, Brazil.

**Figure 2.** Predicted habitat occupancy by *Antirrhea ulei* across sample sites at Uei Tepui, according to a Bayesian hierarchical occupancy model. The logit transformation of *A. ulei* probability of habitat occupancy (y-axis; *A. ulei*  $\psi$ ) was modelled as a linear function of several environmental gradients summarised by the first axis of a PCA ordination (x-axis; PCA 1). The species mean probability of occurrence (black line) increases markedly with increasing values of the PCA 1 axis. Light green lines represent all models fitted according to posterior estimates and the higher density of lines indicates the area with higher model confidence.

**Figure 3.** Predicted habitat occupancy by *Antirrhea ulei* in Eastern Tepuis, according to a Bayesian hierarchical-occupancy model. (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (b). (b) Map of Eastern Pantepui showing the predicted habitat occupancy by the species and localities mentioned in the text; white rectangle enlarged in (c). (c) Map of Uei Tepui showing the predicted habitat occupancy by the species and sampling plots location. Black points show plots where the species was present, whereas white points show plots where the species was not detected. (d) Aerial view of the northern face of Uei Tepui, showing tepui summit and lower forested slopes. The model was fitted to data collected in Uei Tepui (c) and then extrapolated to the extent of the Eastern tepuis (b). 1. Uei Tepui; 2. Roraima Tepui; 3. Kukenán Tepui; 4. Karaurin Tepui; 5. Sierra de Lema; 6. Auyán Tepui; 7. Chimantá Massif; 8. Mount Wokomong; 9. Mount Ayanganna; 10. Merume Mountains. Photo: Thiago Laranjeiras.

**Figure 4.** Current and historical predicted distribution of *Antirrhea ulei*. (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (b). (b) Map of Eastern Pantepui showing the current and past predicted distribution of the species and localities mentioned in the text. Binary prediction of habitat occupancy was

set at threshold of 0.5 of probability of occupancy. Historical prediction was based on climatic conditions during the last glacial maximum (LGM) according to the Community Climate System Model (CCSM; Lima-Ribeiro et al., 2015). 1. Uei Tepui; 2. Roraima Tepui; 3. Kukenán Tepui; 4. Karaurin Tepui; 5. Sierra de Lema; 6. Auyán Tepui; 7. Chimantá Massif; 8. Mount Wokomong; 9. Mount Ayanganna; 10. Merume Mountains.

## Capítulo II.

**Figure 1.** Distribution of sample plots in várzea and terra firme forests. Maps show the distribution of sampling plots overlapped with an elevation Radar image from the Shuttle Radar Topography Mission (SRTM). Black rectangles in the left map are enlarged in right panels (A–C).

**Figure 2.** Butterfly counts and number of species in várzea and terra firme forest plots. Difference in butterfly counts (A) and number of species (B) per plot between the two forest types. Square, circle and triangle symbols represent plots in Baixo Juruá, Mamirauá and Amanã reserves, respectively. (C) Assemblage rank-abundance distribution from the two forest types.

**Figure 3.** Butterfly richness estimated by rarefaction (solid curves) and extrapolation (dashed curves) based on sample size (A) and completeness, (B) with corresponding 95% confidence intervals (shaded areas). Solid circles indicate the observed species richness and open circles indicate the extrapolated richness in terra firme assemblages based on number of individuals (A) or sample coverage. (B) Numbers within parentheses indicate the coordinates in both graphs. Although estimated richness in várzea seems to be higher than terra firme at its maximum sample size (731 individuals in “A”) or completeness (0.97 of coverage in “B”), the confidence intervals overlap and indicate there is no statistically significant difference in richness between the two forest types.

**Figure 4.** Changes in species composition between várzea and terra firme forests. (A) Butterfly species composition in a bi-plot with the two axes derived from a NMDS ordination. Each point in the graph represents a plot located in várzea or terra firme forest and the distance between points represents the similarity of plots in terms of their species composition. Square, circle, and triangle symbols represent plots in Baixo Juruá,

Mamirauá, and Amanã reserves, respectively. (B) Distribution of butterflies across sample sites. Sample sites are ordered by a single NMDS axis and bar heights show the relative abundance of butterfly species across várzea (gray) and terra firme (black) plots. (C) Change in species composition (NMDS 1) with environmental gradients (PCA 1) along and within each forest type, after controlling for the effects of latitude and longitude.

### Capítulo III.

**Figure 1.** Distribution of sampling plots across Amazonia. White squares show the location of sampling grids and adjacent numbers indicate the number of sampling plots surveyed in each grid.

**Figure 2.** Independent responses of species richness and composition (y-axes) to climatic variables (x-axis). Graphs represent the partial responses according to multiple regression models.

**Figure 3.** Ordination plots according to a Principal Coordinate Analysis (PCoA) to summarize similarities in Amazonian butterfly assemblages. Distance between points represent their similarity between plots according to their species composition. Colors in the left graph represent the major bird areas of endemism, and distance among group centroids may be interpreted as differences in species composition among groups. Arrows length in the right graph show the correlation of variables with PCoA 1 or 2. Black and blue arrows indicate significant and non-significant correlations of variables and PCoA axes, respectively. lat = latitude; long = longitude; sol.rad = mean annual solar radiation; temp = mean annual temperature; prec = annual precipitation; cation = soil cation concentration; clay = soil clay content; trecov = % of tree cover; canopy = canopy height.

**Figure 4.** Venn diagram showing the relative contribution ( $R^2$ ) of geographical position (Geo); environmental variables (Env) and areas of endemism (AoE) to explain butterfly compositional turnover in Amazonia. Compositional turnover was measured by a Principal Coordinate Analysis (PCoA), based on the Jaccard index. Relative contributions were determined using multiple regressions and variance partitioning.

Values show the amount of variance that was uniquely or jointly explained by the components. Components with  $R^2 < 0$  are not shown.

**Figure 5.** Decay of compositional dissimilarity with geographical distance and environmental difference among 148 sample plots. Each gray point represents a pair of sites being compared. Butterfly similarity (Jaccard index) between sites are plotted against their geographical and environmental distances in left and middle graphs. Environmental similarity between sites is plotted against their geographic distance in the right graph. Environmental similarity is the complement of the environmental distance. Linear, logarithm and flexible splines curves are shown to represent changes in the average similarity with increasing distance. Flexible spline function gives the most accurate representation of changes in average similarity.

## Introdução geral

A ocorrência de uma espécie em um determinado local é influenciada por fatores históricos, ecológicos e evolutivos, sendo determinada por filtros de dispersão, ambientais e bióticos (Leibold *et al.*, 2004). Estes filtros afetam a distribuição de espécies em diferentes escalas espaciais e podem agir em conjunto ou separadamente. Em escalas espaciais mais amplas, os fatores geométricos (i.e., distância e posição geográfica) e as barreiras geográficas impedem que as espécies ocorram em todos os lugares, através de mecanismos de limitação de dispersão – as espécies só ocorrem onde conseguem chegar de acordo com sua capacidade de dispersão. Quando as espécies são capazes de dispersar para um determinado local, restrições ambientais podem impedir o estabelecimento das espécies localmente, devido aos requerimentos e tolerâncias da espécie aos gradientes ambientais. Por fim, em escalas geográficas locais, quando as espécies são capazes de se dispersar e as condições ambientais são adequadas, a distribuição de espécies pode ainda ser influenciada por interações bióticas com competidores e/ou predadores, impedindo ou diminuindo as chances da espécie ocorrer localmente.

A pressão seletiva de fatores ambientais podem selecionar a evolução de características adaptativas, o que por sua vez pode afetar a capacidade das espécies de dispersar e persistir em escalas locais. Esse pode ser o caso de espécies com alto grau de endemismo, que possuem requerimentos ambientais específicos de acordo com o ambiente em que ocorrem. Nas montanhas remotas do escudo das Guianas, por exemplo, uma complexa dinâmica de sucessivas mudanças climáticas resultou em diversos eventos vicariantes e de migração, dando origem a uma biota altamente adaptada, com um elevado número de espécies endêmicas, restritas às altas altitudes (Rull & Vegas-Vilarrúbia, 2019). Dessa forma, a reconstrução histórica das mudanças nos padrões de distribuição de espécies em resposta aos fenômenos biogeográficos, permanece sendo uma questão aberta em ecologia e evolução, sendo também um importante desafio da biogeografia moderna.

Em escalas locais, os filtros ambientais tendem a atuar junto com filtros bióticos para determinar a abundância, o número e a composição de espécies (Leibold *et al.*, 2004). Para espécies dependentes de floresta, o tipo de vegetação costuma ser a característica biótica mais frequentemente utilizada para associar à distribuição espacial

das espécies. As florestas de várzea da Amazônia Central, por exemplo, são inundadas sazonalmente por águas ricas em nutrientes, que fertilizam o solo e aumentam a produtividade primária da floresta (Irion *et al.*, 2010). Essa maior entrada de nutrientes em longo prazo pode afetar a abundância e a riqueza de espécies, por mecanismos *bottom-up*, onde os nutrientes são absorvidos por níveis tróficos mais baixos e transferidos para os níveis mais altos ao longo da cadeia trófica. Por outro lado, a inundação da floresta pode ser um fator ambiental limitante para a ocorrência de espécies que não toleram o alagamento, determinando a distribuição dessas espécies, bem como de outras espécies com as quais interagem (e.g., predadores/competidores).

Em escalas espaciais mais amplas, a distribuição espacial das espécies é resultado de efeitos sinérgicos de sua capacidade de dispersão, a qual impede que as espécies ocorram em todos os lugares (Hubbell, 2001), e de restrições ambientais, que resultam em distribuições irregulares de espécies ambientalmente adaptadas (Tuomisto *et al.*, 2003). Por isso, associar os padrões de distribuição das espécies a processos históricos ou ambientais subjacentes é muitas vezes desafiador, pois a distribuição das espécies é dinâmica e muda constantemente por diversas razões (Warren *et al.*, 2014). Na Amazônia, os grandes rios são as barreiras potenciais mais óbvias à dispersão de espécies terrestres, e foram reconhecidos como limites de distribuições para vários grupos de vertebrados (por exemplo, aves terrestres, Ribas *et al.* 2012; primatas, Boubli *et al.* 2015; e lagartos, Dias-Terceiro *et al.* 2015). No entanto, para espécies com maior capacidade de dispersão, os grandes rios são barreiras menos óbvias, tais como plantas (Tuomisto *et al.*, 2003) e insetos (Penz *et al.*, 2015; Dambros *et al.*, 2017; Guilherme *et al.*, 2021), e a distribuição dessas espécies tende a ser mais fortemente limitada pelas condições ambientais (Hubbell, 2001). Dessa forma, a importância relativa dos fatores ambientais e de dispersão pode variar de acordo com o grupo taxonômico avaliado (Dambros *et al.*, 2020).

As borboletas são animais abundantes nas florestas tropicais e estão fortemente associadas a seus habitats em todos os estágios da vida (Freitas *et al.*, 2006). A guilda de borboletas frugívoras constitui um grupo não monofilético de algumas subfamílias de Nymphalidae, e compreende até 75% de todos os ninfalídeos neotropicais (Brown 2005). Essas espécies ganham a maior parte de suas necessidades nutricionais a partir de frutos apodrecidos, seiva de plantas e outros materiais orgânicos em decomposição, o que permite uma amostragem fácil e simultânea com armadilhas e iscas atrativas. Além

disso, essa guilda pode funcionar como um bom grupo indicador de outros grupos biológicos, uma vez que riqueza e diversidade locais estão correlacionadas com a diversidade total de borboletas (Brown and Freitas 2000) e com vários outros artrópodes, vertebrados, árvores e lianas (Barlow *et al.*, 2008; Gardner *et al.*, 2008).

Na Amazônia, os gradientes ambientais de topografia e vegetação representam mudanças na disponibilidade de recursos alimentares e nas condições físicas do ambiente para as borboletas, afetando diretamente a distribuição espacial das espécies em escalas locais (Ribeiro & Freitas, 2012; Graça *et al.*, 2015, 2017). Portanto, mudanças ambientais podem filtrar espécies do *pool* regional, determinando a riqueza e composição de espécies local. Ao contrário de muitas espécies de vertebrados, as borboletas podem se dispersar rapidamente e a grandes distâncias (Penz *et al.*, 2015). Embora vários gêneros sejam distribuídos globalmente, as florestas tropicais abrigam maior diversidade (Legg, 1978), o que sugere que o clima também afeta a distribuição de espécies em escalas mais amplas (Menéndez *et al.*, 2007; Stefanescu *et al.*, 2011; Santos *et al.*, 2020), embora nenhum estudo de ampla escala tenha sido realizado na Amazônia.

Nesse contexto, no Capítulo I dessa tese eu usei uma abordagem de modelagem de ocupação para prever o padrão atual e histórico da distribuição de *Antirrhea ulei* – uma espécie de borboleta rara e endêmica do Pantepui, no norte da Amazônia. Especificamente, eu avaliei como os gradientes ambientais afetam o padrão de ocupação do habitat da espécie, reconstruindo a distribuição histórica e atual da espécie, de acordo com seus requerimentos ambientais, desde o último máximo glacial (LGM; ~21.000 anos atrás). No Capítulo II, eu comparei as assembleias de borboletas de florestas de várzea e terra firme na Amazônia Central, testando se abundância, riqueza e composição de espécies difere entre esses dois tipos florestais. Além disso, avaliei o papel da inundação das florestas, e seus gradientes ambientais associados entre e dentro desses tipos florestais, na estrutura da assembleia. Por fim, no Capítulo III, eu investiguei como a riqueza e composição de espécies de borboletas frugívoras estão associadas aos fatores geométricos, às regiões biogeográficas delimitadas por rios, e aos gradientes ambientais (clima, solo e vegetação) em amplas escalas geográficas na Amazônia. Ainda, avaliei a importância relativa da limitação de dispersão (isolamento por distância ou barreiras geográficas) e de filtragem ambiental no padrão de distribuição das espécies em amplas escalas.

## Objetivos

Avaliar a influência de filtros de dispersão, ambientais e bióticos na distribuição de borboletas frugívoras em diferentes escalas espaciais na Amazônia.

### Objetivos específicos

- Capítulo I: avaliar como os gradientes ambientais afetam a distribuição espacial de *Antirrhea ulei*, uma borboleta endêmica do Pantepui, bem como avaliar como as mudanças históricas no padrão de distribuição espacial da espécie foram influenciadas pelas flutuações climáticas desde o último máximo glacial (LGM; ~21.000 anos atrás).
- Capítulo II: avaliar como a inundação das florestas (filtro ambiental) e o tipo florestal (filtro biótico) influenciam a abundância, riqueza e estrutura da assembleia de borboletas em escalas locais.
- Capítulo III: investigar como a limitação por dispersão (devido a fatores geométricos e barreiras biogeográficas) e a filtragem ambiental afetam a riqueza e composição de espécies de borboletas, bem como avaliar a importância relativa desses fatores como determinantes da distribuição espacial das espécies em amplas escalas geográficas na Amazônia.

## Capítulo I.

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Rabelo, R.M.; Oliveira, I.F.; Magnusson, W.E. **Finding a lost species in the “Lost World”: predicted habitat occupancy by an endemic butterfly in a Neotropical sky-island archipelago.** Publicado em *Insect Conservation and Diversity*.



# Finding a lost species in the ‘Lost World’: predicted habitat occupancy by an endemic butterfly in a Neotropical sky-island archipelago

RAFAEL M. RABELO,<sup>1,2</sup>  ISABELA FREITAS OLIVEIRA<sup>1</sup> and WILLIAM E. MAGNUSSON<sup>1</sup>

<sup>1</sup>Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil and <sup>2</sup>Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Brazil

**Abstract.** 1. Pantepui is a Neotropical archipelago of remote sky islands (tepui) that harbours a unique and poorly known biota, such as the endemic butterfly *Antirrhea ulei*. The Vicariance-Migration hypothesis argues that Pantepui biota originated from a complex succession of climatic shifts, causing up-and-down migrations of cool-adapted species from the last glacial maximum (LGM) to the present.

2. We evaluated how environmental gradients affect *A. ulei* habitat occupancy and predict its distribution across the Eastern Pantepui. We also test whether the species had a broader distribution during the LGM, following the Vicariance-Migration hypothesis.

3. We surveyed for butterflies across 14 plots at Uei tepui, following an elevational gradient. We used Bayesian occupancy modelling to evaluate how environmental gradients affect *A. ulei* occurrence and to predict the current and past species distribution.

4. Species habitat occupancy was strongly associated with environmental gradients. Our model correctly predicted the species occurrence at all localities previously reported to be occupied by the species, and also predicted the potential species occurrence on other tepuis. Our historical prediction of species distribution showed that the species likely had a broader distribution during the LGM, in comparison with its current restricted distribution.

5. Our historical predictions suggest that the species may have spread across the Eastern Pantepui during LGM and migrated up the tepuis during the Holocene warming, in accordance with the Vicariance-Migration hypothesis. Our study shows how data from local standardised surveys can be useful to estimate the distribution pattern of other little-studied species of the Pantepui biota.

**Key words.** *Antirrhea*, Bayesian occupancy model, detectability, endemism, last glacial maximum, Pantepui, species distribution modelling, Vicariance-Migration hypothesis.

## Introduction

The Guayana Highlands hold one of the most impressive and pristine scenic landscapes on Earth – the Pantepui. It is an archipelago of sky islands, located between the Orinoco and Amazon rivers, formed by remote table mountains (locally called

tepui) of 1500–3000 m in elevation, with flat and nearly inaccessible summits that vary from 1 to approximately 1000 km<sup>2</sup> (Rull & Vegas-Vilarrúbia, 2020). The tepui summits are remnants of Precambrian surfaces (sandstones and quartzites), which have undergone successive erosions until the Pleistocene, creating table-top mountains (Briceño & Schubert, 1990).

Palaeoecological records have shown that the Pantepui biota originated from a complex succession of climatic shifts, which caused up-and-down migrations of species from the last glacial maximum (LGM; ~21 000 years ago) to the present

Correspondence: Rafael M. Rabelo, Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, Manaus, Amazonas 69067-375, Brazil. E-mail: rmrabelo@gmail.com

(Rull, 2005; Rull *et al.*, 2019). In this context, Pantepui cool-adapted species could have migrated downwards during glacials, seeking their particular climatic requirements and tolerances. Once spread across lowlands and uplands, these species would have had the possibility of climbing several tepuis during the Holocene warming (the last 11 700 years). Therefore, Quaternary climatic fluctuations probably triggered the Pantepui biota to disassemble during glacials and reassemble during inter-glacials, playing a significant role in Pantepui biogeography (Rull & Vegas-Vilarrúbia, 2019). However, it is worth noting that these up-and-down migrations are a complex process, which depends on the topography of each tepui and idiosyncrasies of each species (Rull & Vegas-Vilarrúbia, 2020).

The biogeographical context of Pantepui gave rise to its astonishing biodiversity with a high number of endemic species of flora and fauna (Rull & Vegas-Vilarrúbia, 2019). It was the uniqueness of these plant and animal species, discovered during the first expeditions to this hitherto new and strange environment in the late 19th century that likely inspired Sir Arthur Conan Doyle to write the famous novel entitled 'The Lost World'. One example of such a unique species is *Antirrhea ulei* (Strand, 1912) – a butterfly species considered to be endemic to the tepuis (Fig. 1). This species was described based on a female specimen collected by the botanist Ernst Ule during an expedition to Roraima Tepui in the early 20th century (Strand, 1912). However, a large amount of biological material from the Berlin museum, where the specimen was deposited, was destroyed during the Second World War, and the type of *A. ulei* was considered lost (Orellana, 2004). Thus, a new specimen of the same sex from Sierra de Lema was chosen to designate the neotype (Orellana, 2004).

Information on the distribution of *A. ulei* is scarce and species records are limited to few tepuis. To the best of our knowledge, the species has been found at only the following tepuis: Roraima Tepui (type – Strand, 1912), Sierra de Lema (neotype) and Auyán Tepui (Orellana, 2004), Mount Wokomung (Fratello, 1996) and Mount Ayanganna (Fratello, 1999). The species occurs in the cloud forests of these tepuis at elevations above 1200 m and its larvae

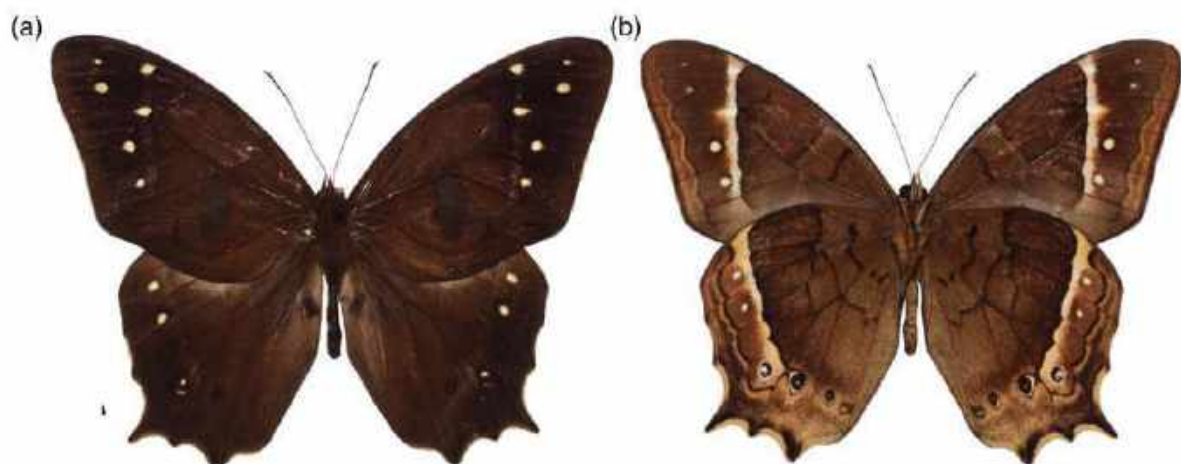
probably feed on *Prestoea* palms (Orellana, 2004), which are commonly found at elevations above 1000 m in the Guayana Highlands (Henderson & Galeano, 1996). It is difficult to draw conclusions about the ecology or evolutionary processes that may have affected these species with limited empirical knowledge. In such cases, species-distribution modelling can help to explain how environmental factors affect the species habitat occupancy, to predict the current pattern of species distribution, identifying potential tepuis for species occupancy, as well as reconstructing its historical distribution. Understanding historical patterns of species distribution, especially those strongly associated with specific habitats, such as butterflies, can help to understand the origin of Pantepui biota.

Here we use an occupancy-modelling approach to predict the current and historical pattern of *A. ulei* distribution across the Eastern Pantepui. Specifically, we (i) evaluate how environmental gradients affect the species' habitat occupancy at Uei Tepui, (ii) map the current species distribution based on its ecological requirements across the Eastern Pantepui, and (iii) test whether the species had a broader distribution during the LGM, when the climate now found on the Pantepui likely had a wider extent, following the Vicariance-Migration hypothesis (Rull, 2005). We expect that *A. ulei* environmental requirements are restricted to highlands, and that our model may be validated by the previous records of the species in other tepuis, as well as help to identify potential non-surveyed tepuis for species occurrence. We also expect to find that the species had a broader range during the LGM, which represents the typical Quaternary glaciation, suggesting that the species may have spread across the eastern Pantepui during glacials, and migrated upwards to the current tepuis during the Holocene warming.

## Materials and methods

### Study area

Our study region comprises the Eastern portion of Pantepui. Sampling was undertaken at Uei Tepui (5°5'N, 60°35'W), in



**Fig 1.** Dorsal (a) and ventral (b) view of a male specimen of *Antirrhea ulei* collected at Uei Tepui, Roraima State, Brazil.

Roraima, the northernmost state of Brazil. Uei Tepui is located on the border of Brazil and Venezuela, has a maximum elevation of 2150 m, with a summit area of 2.5 km<sup>2</sup> and a slope area of 20 km<sup>2</sup> (Rull & Vegas-Vilarrúbia, 2020). Uei Tepui is protected by the Raposa Serra do Sol Indigenous Land and by the Monte Roraima National Park (ICMBio, FUNAI).

Meteorological data for Pantepui are scarce, but available data from three weather stations over a period of 12 years (1997–2009) allow some generalisation to be made (Rull & Vegas-Vilarrúbia, 2020). Annual average temperature ranges between 11.4 °C and 16.5 °C with a general elevational decrease of approximately 0.6 °C/100 m. Annual precipitation ranges from 280 to 5300 mm, and increases with elevation at a rate of 30 mm/100 m. Moisture is also provided by common dense mists. Precipitation may vary throughout the year, with rainfall being less common from December to March.

### Sampling design and data collection

We surveyed butterflies in 14 plots at the beginning of the dry season (November–December 2019). Plots (sample units) consisted of 200-m long transects. Most plots were separated by at least 1 km from one another, but some higher elevation plots were separated by only 400 m due to logistical constraints.

Butterfly surveys were conducted via passive sampling, by placing eight baited butterfly traps along the centreline of each plot. At each 50 m, we hung two traps on tree branches, one in the forest understory (1–1.5 m high) and one in the canopy (15–25 m high). We baited the traps with a mixture of sugarcane juice and bananas fermented for 48 h (Freitas *et al.*, 2014) and visited them every 48 h to check for captures and replace the bait. We left the traps active for 6–12 consecutive days (Supporting Information Table S1). All captured individuals were collected for posterior species identification and the specimens were deposited in the Entomological Collection of the National Institute for Amazon Research, Manaus, Brazil.

We gathered topographic, vegetation and climate data from GIS databases (Supporting Information Table S2). We obtained current climate data from WorldClim v.2 (Fick & Hijmans, 2017) and the LGM simulation of climate scenario from the Community Climate System Model (CCSM), developed by the Coupled Modeling Intercomparison Projects (CMIP5) and Paleoclimate Modeling Intercomparison Projects (PMIP3) available from the ecoClimate database (Lima-Ribeiro *et al.*, 2015). As most of these variables were highly correlated with each other, we summarised the environmental data with a principal component analysis (PCA). The first axis derived from this ordination was highly correlated ( $r > |0.5|$ ) with most of the environmental variables (Supporting Information Table S2), so we used this axis (PCA 1) to represent the environmental variables in our model.

### Data analysis

We assessed the pattern of *A. ulei* occurrence across our sample sites using an occupancy-modelling approach. This approach estimates the probability of a site being occupied/used ( $\psi$ ) by a

given species when its detection probability is less than 1 (Mackenzie *et al.*, 2006). Given that the non-detection of a species at a sample site results from either its true absence or the failure to detect it, repeated surveys (occasions) on multiple sample sites are used to estimate the detection probability ( $P$ ) of a species conditional on occupancy. In our model, *A. ulei* occurrence at a given site ' $i$ ' is denoted as  $O_i$  (i.e., the true occupancy state: 1 if present, 0 otherwise), and is the outcome of a Bernoulli trial with probability of occupancy  $\psi_i$ .

$$O_i \sim \text{Bernoulli}(\psi_i)$$

Similarly, the binomial detection/non-detection (1 = present; 0 = not detected) of the species ( $D$ ) during a given occasion ' $j$ ' and in a given sample site ' $i$ ' are input in the form of an array  $D_{ij}$ . Therefore, whether the species is detected during a given occasion in a given site is conditional on the occupancy state  $O_i$ , as follows:

$$D_{ij} \sim \text{Bernoulli}(P_{ij} * O_i)$$

where  $P_{ij}$  is the probability of species detection during an occasion (survey) in a site. We substituted time for space and considered each of the four pairs of traps (understory and canopy) in each sampling plot as a sampling occasion (Supporting Information Table S1).

We estimated both  $\psi$  and  $P$  parameters as linear responses to predictor variables using a logit link function in a regular logistic model. As the sampling effort differed across plots, we added the sampling effort on each sampling plot (values were standardised before running the model) into the model as a detection covariate; that is, we expected that the longer the sampling period, the higher the likelihood of detecting *A. ulei* in traps. We modelled the logit transformation of detection probability as follows:

$$\text{logit}(P_{ij}) = \alpha_0 + \alpha_1 * \text{sampling effort}_{ij}$$

We then considered that the occupancy probability  $\psi_i$  depended on the combination of environmental factors on site ' $i$ ' (i.e., PCA 1 scores for each site), in a logit transformation of a linear model as follows:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 * \text{PCA1}_i$$

The full hierarchical model formulation is given in Supporting Information Fig. S1. We implemented the model in a Bayesian framework using JAGS accessed via the software R, version 3.4.4 (R Development Core Team, 2018) using the package 'rjags' (Plummer, 2016) (see the R code available in Appendix S1 in Supporting Information). We used vague priors for all model parameters. We used logistic priors for intercepts [ $\alpha_0$  and  $\beta_0 \sim \text{Logistic}(\mu = 0, \sigma = 1)$ ], which imply a Uniform(0, 1) prior for  $P$  and  $\psi$  in the probability scale, when covariates are equal to zero (Northrup & Gerber, 2018). We used normal priors with mean = 0 and variance = 10 for the regression coefficients [ $\alpha_1$  and  $\beta_1 \sim \text{Normal}(\mu = 0, \sigma = 3.16)$ ] describing the effects of covariates detection and occupancy probabilities in the logit scale. We conducted a prior sensitivity analysis, using

sequentially smaller values of  $\sigma$ , and found no differences in posterior estimates of model coefficients, nor in detection and occupancy probabilities (Supporting Information Fig. S2). We estimated posterior parameters with the Markov Chain Monte Carlo (MCMC) method using three parallel MCMC chains of 100 000 in length after discarding the first 10 000 steps of each as burn-in, and with a thinning rate of 100 steps. This combination of values ensured that all chains converged, that is, essentially oscillated around the same mean parameter value (see Supporting Information Fig. S3). We report the posterior distribution of all estimated parameters as means and standard errors (SEs), as well as the medians and the 2.5 and 97.5 percentiles, which are the Bayesian equivalent to the 95% confidence interval [highest posterior density in 95% (HPD95)].

## Results

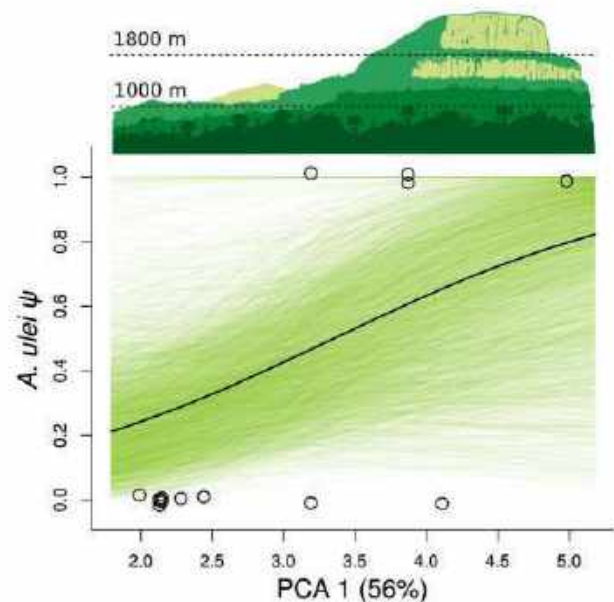
We obtained a total of 12 *A. ulei* independent detections at four (29%) of the 14 sample sites during four sampling occasions. The mean detection probability across sites was  $P = 0.56$  (HPD95: 0.3–0.83), and it was not influenced by differences in sampling effort (Table 1). The mean probability of site occupancy was  $\psi = 0.41$  (HPD95: 0.24–0.75), and it was affected by the environmental gradients summarised by the first PCA axis (Table 1; Fig. 2). Higher values of PCA 1 axis were associated with higher elevation, tree cover and canopy height, but also with lower temperatures and seasonal variation in temperature and precipitation (Supporting Information Table S2). PCA 1 axis captured 56% of the variation in environmental variables.

According to our model predictions, the species has a high probability of habitat occupancy on several Eastern tepuis (Fig. 3). Our model correctly predicted the species occurrence at all five localities previously reported to be occupied by the species: Roraima Tepui (type locality), Sierra de Lema (neotype), Auyán Tepui, Mount Ayanganna and Mount Wokomong. Our model also predicted the potential species occurrence at other tepuis of the Eastern chain, at Northwest of Roraima Tepui (e.g., Kukenán and Karaurín tepuis), at Chimantá massif, in Venezuela, and at Merume Mountain, in Guyana.

**Table 1.** Parameter estimates (link scale) from the hierarchical occupancy model for *Antirrhea ulei* occurrence at Uei Tepui in Raposa Serra do Sol Indigenous Territory.

| Parameter  | Estimate (SE) | 2.5%  | Median | 97.5% |
|------------|---------------|-------|--------|-------|
| $\alpha_0$ | 0.30 (0.02)   | –1.71 | 0.30   | 2.01  |
| $\alpha_1$ | 0.89 (0.02)   | –1.43 | 0.89   | 3.12  |
| $\beta_0$  | –2.81 (0.03)  | –6.82 | –2.71  | 0.55  |
| $\beta_1$  | 0.84 (0.01)   | –0.22 | 0.79   | 2.18  |

$\alpha_0$  and  $\alpha_1$  are the coefficients (intercept and slope, respectively) of a logistic model of *A. ulei* detection probability  $P$ ;  $\beta_0$  and  $\beta_1$  are the coefficients (intercept and slope, respectively) of a logistic model of *A. ulei* probability of occurrence  $\psi$ . See full model formulation in Supporting Information Fig. S1.

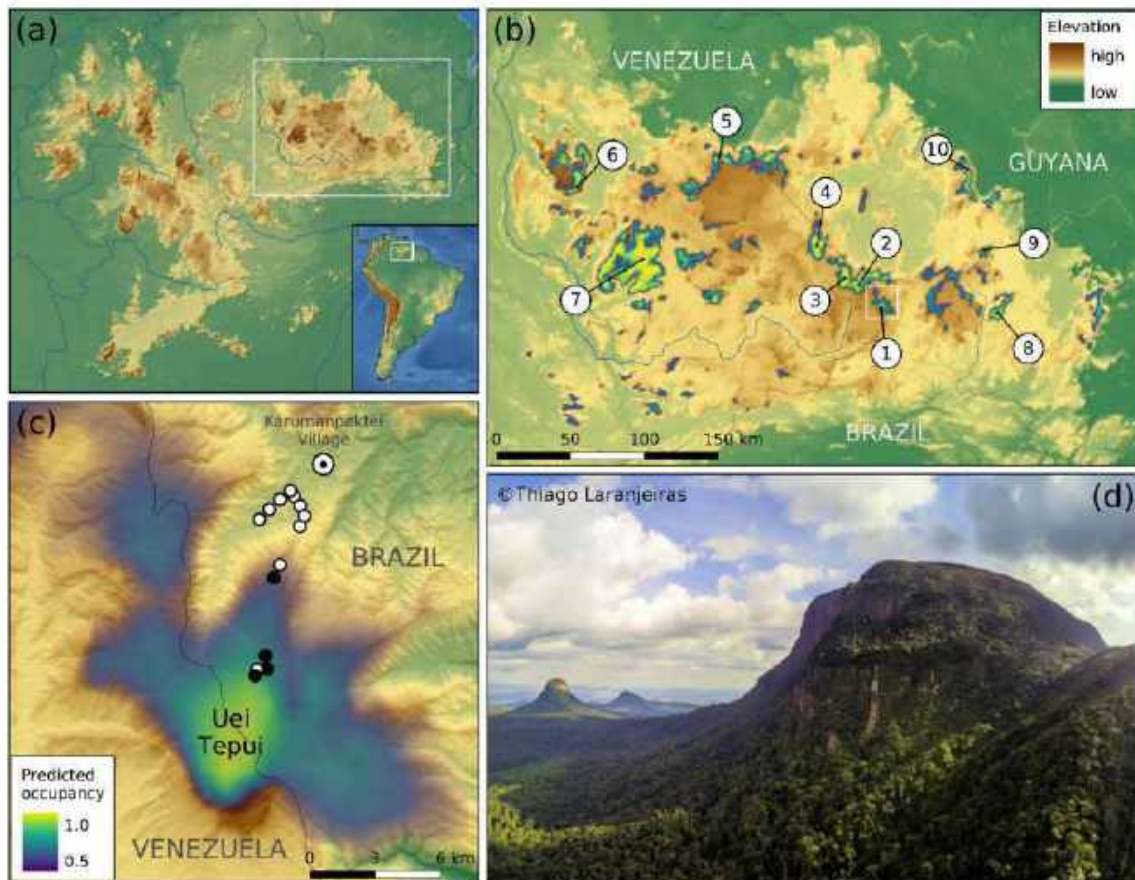


**Fig 2.** Predicted habitat occupancy by *Antirrhea ulei* across sample sites at Uei Tepui, according to a Bayesian hierarchical occupancy model. The logit transformation of *A. ulei* probability of habitat occupancy (y-axis;  $A. ulei \psi$ ) was modelled as a linear function of several environmental gradients summarised by the first axis of a PCA ordination (x-axis; PCA 1). The species mean probability of occurrence (black line) increases markedly with increasing values of the PCA 1 axis. Light green lines represent all models fitted according to posterior estimates and the higher density of lines indicates the area with higher model confidence.

Our prediction of the historical change in the distribution of the species is shown in Fig. 4. According to our model, the species likely had a wider distribution during the LGM and populations were probably more connected to each other, even though the species already had a patchy pattern of occurrence, restricted to the highlands of the Eastern Pantepui. As the climate started to warm during the Holocene, the species lost part of its suitable habitat at lower elevations, being restricted to the higher areas, where the tepuis are currently found.

## Discussion

We found that *A. ulei* has higher probability of occurrence at higher values of our environmental gradients (PCA 1), that is, in habitats at higher elevations (above ~1400 m), with a high percent of tree cover and with taller forests, but also with lower temperatures and less seasonal variation in temperature and precipitation. A higher probability of occurrence of the species at the forested habitats of tepuis is expected, since this is a forest-dwelling species that occurs in the lower strata of the forest (Orellana, 2004). Besides, the common host plants for *Antirrhea* butterflies are mainly palms from the genus *Prestoea*, *Euterpe*, *Oenocarpus*, *Geonoma* and *Calyptranthes* (Heredia & Alvarez-lopez, 2004; Beccaloni *et al.*, 2008), which can be abundant in forested habitats in tepuis (Henderson & Galeano, 1996), but



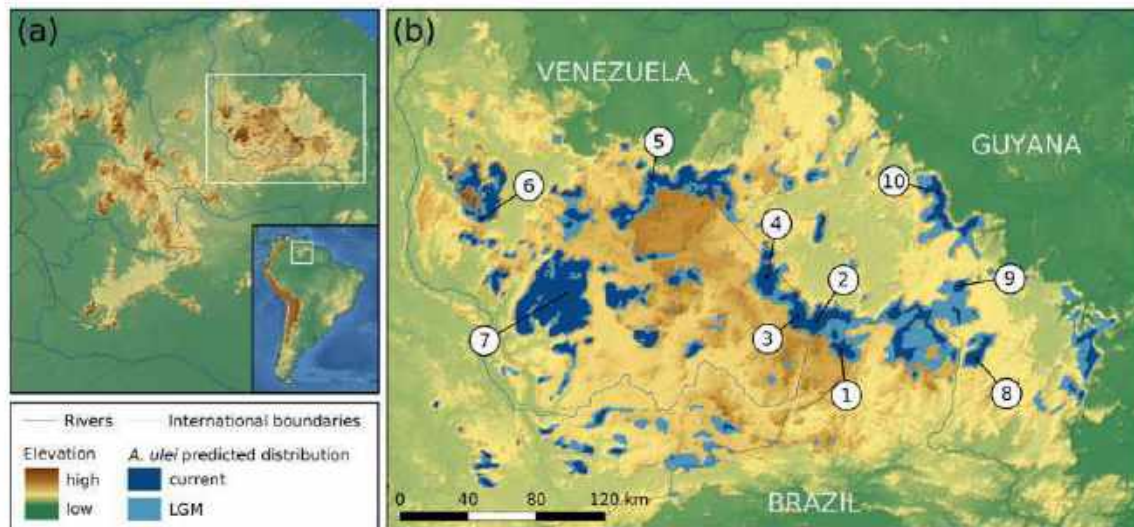
**Fig 3.** Predicted habitat occupancy by *Antirhea ulei* in Eastern Tepuis, according to a Bayesian hierarchical-occupancy model. (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (b). (b) Map of Eastern Pantepui showing the predicted habitat occupancy by the species and localities mentioned in the text; white rectangle enlarged in (c). (c) Map of Uei Tepui showing the predicted habitat occupancy by the species and sampling plots location. Black points show plots where the species was present, whereas white points show plots where the species was not detected. (d) Aerial view of the northern face of Uei Tepui, showing tepui summit and lower forested slopes. The model was fitted to data collected in Uei Tepui (c) and then extrapolated to the extent of the Eastern tepuis (b). 1. Uei Tepui; 2. Roraima Tepui; 3. Kukenán Tepui; 4. Karaurin Tepui; 5. Sierra de Lema; 6. Auyán Tepui; 7. Chimantá Massif; 8. Mount Wokomong; 9. Mount Ayanganna; 10. Merume Mountains. Photo: Thiago Laranjeiras.

are rare or nearly absent in the shrub and herbaceous vegetation of tepui summits (pers. observ.). Butterfly distribution is strongly associated with vegetation; therefore, the presence of the host plant is one (and perhaps the most) important biotic factor limiting the species occurrence (DeVries, 1986; Koh *et al.*, 2004). In fact, butterfly endemism appears gradually from the middle elevations (~1000 m), at the montane level, and increases notably with altitude, especially above 1500 m, when vegetation switches to upper montane with high degree of endemism in plants (Viloria & Costa, 2019).

Our sampling at Uei Tepui did not cover the whole range of tepui environmental variation. As we moved from 1000 to 1800 m (the approximate elevation range our sampling covered), vegetation structure changed from submontane-to-montane dense forests to ~7-m tall cloud forests with gnarled tree trunks covered with mosses and a dense, nearly impenetrable understory. At the highest elevation we established a plot (1820 m), forest canopy was very short, so we were only able to install traps

in the understory. Above this elevation, at Uei Tepui summit, the vegetation changed drastically to a mosaic of shrub and herbaceous vegetation on a bare rock substrate, with very sparse small trees, on which we could not hang traps. We have opportunistically surveyed the Uei Tepui summit with insect nets, but we did not detect any *A. ulei* individuals, nor palm species (i.e., their host plants), in these habitats. Therefore, although our model predicts that the species has the highest probability of occurrence at elevations above 1800 m and on tepui summits, our sampling did not cover the environmental variation above this elevation, so we recommend that the predicted presence of species on tepui summits be regarded with caution. We believe that tepui summits are likely not suitable habitats for the species due to their vegetation structure and floristic composition.

Our model correctly predicted the presence of the species in all locations previously described to be occupied by the species and also predicted potential areas for species occurrence on several other tepuis (e.g., Chimantá massif). Although the butterfly



**Fig 4.** Current and historical predicted distribution of *Antirrhoea ulei*. (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (b). (b) Map of Eastern Pantepui showing the current and past predicted distribution of the species and localities mentioned in the text. Binary prediction of habitat occupancy was set at threshold of 0.5 of probability of occupancy. Historical prediction was based on climatic conditions during the last glacial maximum (LGM) according to the Community Climate System Model (CCSM; Lima-Ribeiro *et al.*, 2015). 1. Uei Tepui; 2. Roraima Tepui; 3. Kukenán Tepui; 4. Karaurin Tepui; 5. Sierra de Lema; 6. Auyán Tepui; 7. Chimantá Massif; 8. Mount Wokomong; 9. Mount Ayanganna; 10. Merume Mountains.

surveys in the Pantepui began in the middle of the 19th century (Viloria & Costa, 2019), most of them were opportunistic surveys or surveys that did not follow a standardised sampling protocol. All previous records of species occurrence were opportunistic (Strand, 1912; Fratello, 1996, 1999; Orellana, 2004) and, although there have been butterfly surveys on other tepuis (Viloria & Costa, 2019), they probably failed to detect the species at these locations because they were also opportunistic surveys. To the best of our knowledge, our study represents the first systematic survey of the species, following a standardised sampling protocol and with estimation of detection probability of the species. According to our estimated detection probability ( $P = 0.56$ ), it is expected that opportunistic surveys, or even systematic ones, will often not find the species in a given tepui that it occupies. Future systematic surveys in tepuis we predicted to be occupied by the species would help to understand whether those areas are truly occupied by the species and were not detected in previous surveys, or they represent false positive locations.

Our results suggest that the species likely had a wider distribution during the LGM. With a broader area of suitable habitat available and open migration pathways among tepuis, populations were probably more connected. The current pattern of species distribution suggests that, when the climate warmed during inter-glacials in the Holocene, the suitable habitat at lower elevations became unsuitable and populations may have migrated upwards, becoming isolated on the current tepuis. Therefore, our findings are in accordance with the Vicariance-Migration hypothesis (Rull, 2005), which proposes that glaciations were characterised by the biotic spread of Pantepui sensitive species and inter-glacial upward migration would have favoured vicariance and extinction by habitat loss. We call for studies with

molecular data and/or wing-colour patterns, assessing the differentiation between populations from different tepuis, to confirm such hypothesis, by evaluating whether the divergence time among populations is congruent with LGM. Additionally, we highlight that *A. ulei* distribution may be more strongly associated with its host-plant than with the environmental variables we evaluated, and that its host-plant may not have migrated as fast as the butterfly during glaciations.

Traditionally, Pantepui endemism has been explained by two major speciation processes: ancient vicariance versus recent dispersals, and various hypotheses have been proposed to explain the current distribution of Pantepui biota (Rull, 2019). *Antirrhoea* diverged from other species in the *Morpho* and *Caerois* genera during the Eocene (~38 mya; Wahlberg *et al.*, 2009). It is not known yet whether *A. ulei* originated in the Pantepui or dispersed from somewhere else (e.g., proto-Andes), due to the lack of phylogeographic studies of the genus. In any case, our findings support the idea that Holocene climatic oscillations played an important role in population isolation by vicariance and habitat loss, and may also have had an important role in the diversification of the genus, although genetic data would confirm this hypothesis. A similar model of diversification would have happened with the anurans *Oreophrynella* and *Atelopus*, whose divergence occurred ~40 mya (Eocene) in the proto-Andes and after they dispersed to Pantepui, they diversified there by vicariance (Kok *et al.*, 2018).

This study illustrates how data from local standard surveys can be useful to estimate species ecological requirements and help to understand the distribution pattern of little-studied species. Our model correctly predicted the species occurrence at all localities previously reported to be occupied by the species, and further predicted other potential tepui localities for species

occurrence. Further systematic surveys may help to validate our model predictions. We also found that the species likely had a broader extent of suitable habitat during the LGM and may have spread across the eastern Pantepui, migrating upwards to the current tepuis as its suitable habitat was being lost during the Holocene warming, in accordance with the Vicariance-Migration hypothesis. The framework used in this study can be replicated to other endemics and/or poorly known species to help to understand the evolution of Pantepui biota.

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## Data availability statement

All data that support the findings of this study are available in the Supporting Information of this article.

## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Detection history of *Antirrhoea ulei* across sample sites.

**Table S2.** Variables used in the model.

**Figure S1.** Model formulation.

**Figure S2.** Prior sensitivity analysis on posterior estimates.

**Appendix S1.** R code for model implementation.

**Figure S3.** Chains convergence.

## References

Beccaloni, G.W., Vilorio, Á.L., Hall, S.K. & Robinson, G.S. (2008) Catalogue of the hostplants of the Neotropical butterflies [Catálogo de las plantas huésped de las mariposas neotropicales]. Monografías Tercer

- Milenio. Sociedad Entomológica Aragonesa/Natural History Museum/Instituto Venezolano de Investigaciones, Zaragoza.
- Briceño, H.O. & Schubert, C. (1990) Geomorphology of the Gran Sabana, Guayana Shield, southeastern Venezuela. *Geomorphology*, **3**, 125–141.
- DeVries, P.J. (1986) Hostplant records and natural history notes on Costa Rican Butterflies (Papilionidae, Pieridae & Nymphalidae). *The Journal of Research on the Lepidoptera*, **24**, 290–333.
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315.
- Fratello, S. (1996) Wokomung - a remote Guyana tepui. *Tropical Lepidoptera News*, **2**, 4–5.
- Fratello, S. (1999) Guyana montane expeditions. *Lepidoptera News*, **4**, 4–8.
- Freitas, A.V.L., Iserhard, C.A., Santos, J.P., Carreira, J.Y.O., Ribeiro, D. B., Melo, D.H.A., Rosa, A.H.B., Marini-Filho, O., Accacio, G.M. & Uehara-Prado, M. (2014) Studies with butterfly bait traps: an overview. *Revista Colombiana de Entomología*, **40**, 203–212.
- Henderson, A. & Galeano, G. (1996) *Euterpe*, *Prestoea*, and *Neonicholsonia* (Palmae). *Flora Neotropica*, **72**, 1–89.
- Heredia, M.D. & Alvarez-lopez, H. (2004) Larval morphology and behavior of *Antirrhoea weymeri* Salazar, Constantino & López, 1998 (Nymphalidae: Morphinae) in Colombia. *Journal of Lepidopterists' Society*, **58**, 88–93.
- Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology*, **18**, 1571–1578.
- Kok, P.J.R., Ratz, S., MacCulloch, R.D., Lathrop, A., Dezfulian, R., Aubret, F. & Means, D.B. (2018) Historical biogeography of the palaeoendemic toad genus *Oreophrynella* (Amphibia: Bufonidae) sheds a new light on the origin of the Pantepui endemic terrestrial biota. *Journal of Biogeography*, **45**, 26–36.
- Lima-Ribeiro, M.S., Varela, S., González-Hernández, J., Oliveira, G., Diniz-Filho, J.A.F. & Terrile, L.C. (2015) EcoClimate: a database of climate data from multiple models for past, present, and future for macroecologists and biogeographers. *Biodiversity Informatics*, **10**, 1–21.
- Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. L. & Hines, J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, London, UK.
- Northrup, J.M. & Gerber, B.D. (2018) A comment on priors for Bayesian occupancy models. *PLoS One*, **13**, e0192819.
- Orellana, A.M. (2004) Descripciones y notas taxonómicas sobre *Antirrhoea* Hübner (Lepidoptera: Nymphalidae: Morphinae: Antirrhini). *Entomotropica*, **19**, 21–29.
- Plummer, M. (2016) rjags: Bayesian graphical models using MCMC. R package.
- R Development Core Team (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rull, V. (2005) Biotic diversification in the Guayana Highlands: a proposal. *Journal of Biogeography*, **32**, 921–927.
- Rull, V. (2019) Origin and evolution of the Pantepui biota. *Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands* (ed. by V. Rull, T. Vegas-Vilarrúbia, O. Huber and C. Señaris), pp. 69–91. Elsevier, London, UK.
- Rull, V., Montoya, E., Nogué, S., Safont, E. & Vegas-Vilarrúbia, T. (2019) Climatic and ecological history of pantepui and surrounding areas. *Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands* (ed. by V. Rull, T. Vegas-Vilarrúbia, O. Huber and C. Señaris), pp. 33–54. Elsevier, London, UK.

## 8 Rafael M. Rabelo, Isabela Freitas Oliveira and William E. Magnusson

- Rull, V. & Vegas-Vilarrúbia, T. (2019) Pantepui as a dynamic biogeographical concept. *Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands* (ed. by V. Rull, T. Vegas-Vilarrúbia, O. Huber and C. Señaris), pp. p. 55–67. Elsevier, London, UK.
- Rull, V. & Vegas-Vilarrúbia, T. (2020) The Pantepui "Lost World": towards a biogeographical, ecological and evolutionary synthesis of a pristine Neotropical sky-island archipelago. *Neotropical Diversification: Patterns and Processes* (ed. by V. Rull and A.C. Carnaval), pp. p. 369–414. Springer, Cham, Switzerland.
- Strand, E. (1912) Zwei neue Satyriden von Roraima: gesammelt von Herrn Botaniker E. Ule. *Fauna Exotica*, **2**, 43–44.
- Viloria, Á.L. & Costa, M. (2019) Butterflies. *Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands* (ed. by V. Rull, T. Vegas-Vilarrúbia, O. Huber and C. Señaris), pp. p. 193–222. Elsevier, London, UK.
- Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Pena, C., Nylin, S., Freitas, A.V.L. & Brower, A.V.Z. (2009) Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4295–4302.

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## Capítulo II.

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Rabelo, R.M.; Pereira, G.C.N.; Valsecchi, J.; Magnusson, W.E. **The role of river flooding as an environmental filter for Amazonian butterfly assemblages.** Publicado em *Frontiers in Ecology and Evolution*.



# The Role of River Flooding as an Environmental Filter for Amazonian Butterfly Assemblages

Rafael M. Rabelo<sup>1,2\*</sup>, Geanne C. N. Pereira<sup>2,3</sup>, João Valsecchi<sup>2,4</sup> and William E. Magnusson<sup>1,5</sup>

<sup>1</sup> Programa de Pós-Graduação em Ecologia, National Institute of Amazonian Research (INPA), Manaus, Brazil; <sup>2</sup> Grupo de Pesquisa em Ecologia de Vertebrados Terrestres, Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Brazil;

<sup>3</sup> Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Brazil; <sup>4</sup> Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia (REDEFAUNA), Manaus, Brazil;

<sup>5</sup> Coordenação de Pesquisa em Biodiversidade, National Institute of Amazonian Research (INPA), Manaus, Brazil

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### \*Correspondence:

Rafael M. Rabelo  
mrabelo@gmail.com

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Amazonian flooded (*várzea*) and upland (*terra firme*) forests harbor distinct assemblages of most taxonomic groups. These differences are mainly attributed to flooding, which may affect directly or indirectly the persistence of species. Here, we compare the abundance, richness and composition of butterfly assemblages in *várzea* and *terra firme* forests, and evaluate whether environmental gradients between and within these forest types can be used to predict patterns of assemblage structure. We found that both total abundance and number of species per plot are higher in *várzea* than in *terra firme* forests. *Várzea* assemblages had a higher dominance of abundant species than *terra firme* assemblages, in which butterfly abundances were more equitable. Rarefied species richness for *várzea* and *terra firme* forests was similar. There was a strong turnover in species composition from *várzea* to *terra firme* forests associated with environmental change between these forest types, but with little evidence for an effect of the environmental gradients within forest types. Despite a smaller total area in the Amazon basin, less defined vegetation strata and the shorter existence over geological time of floodplain forests, Nymphalid-butterfly assemblages were not more species-poor in *várzea* forests than in unflooded forests. We highlight the role of flooding as a primary environmental filter in Amazonian floodplain forests, which strongly determines the composition of butterfly assemblages.

**Keywords:** Amazonian floodplains, Lepidoptera, rarefaction, species composition, species density, species richness, *terra firme*, *várzea*

## INTRODUCTION

The number and composition of species at a given site is always a small subset of the regional species pool because environmental and biotic factors act together or separately to filter species from the regional pool and select the species composition at local scales (Hubbell, 2005). Vegetation type is the biotic feature most often used to represent the spatial distribution of forest-dwelling species, and several forest types occur in Amazonian landscapes.

Upland (*terra firme*) forests account for approximately 83% of the Amazon basin (Melack and Hess, 2010) and are located above the maximum seasonal flood levels of rivers, lakes, and large

streams. *Várzea* forests are seasonally flooded by nutrient-rich white-water rivers for 6–8 months, and water-level fluctuations can reach up to 14 m (Junk et al., 2012). *Várzea* forests cover ~7% of the Amazon basin (Melack and Hess, 2010).

*Várzea* and *terra firme* forests harbor distinct assemblages of trees (Wittmann et al., 2004), terrestrial mammals (Alvarenga et al., 2018), bats (Bobrowiec et al., 2014), birds (Beja et al., 2010), litter frogs (Gascon, 1996), and ants (Pringle et al., 2019). Poorer assemblages of several animal groups have been consistently documented in *várzea* forests (Haugaasen and Peres, 2005b; Bobrowiec et al., 2014; Alvarenga et al., 2018; Pringle et al., 2019), suggesting that seasonal inundation explains the lower number of terrestrial and understorey species. In contrast, *terra firme* should have higher species richness than *várzea* forest because it offers more niches associated with the understorey vegetation (Pereira et al., 2009).

It is expected that *terra firme* forests should contain more speciose assemblages of those species groups that can persist in both *várzea* and *terra firme* forests. *Terra firme* forests should have more species than flooded forests since they cover a much larger area (MacArthur and Wilson, 1967), have more stratified vegetation (MacArthur and MacArthur, 1961), and have existed over a longer period of geological time (Ruokolainen et al., 2018). With more species, it is also expected that species abundances in *terra firme* assemblages would be more equitable (MacArthur, 1969). On the other hand, *várzea* forests tend to have higher species abundance/biomass (Haugaasen and Peres, 2005b; Pereira et al., 2009; Pringle et al., 2019) due to the high forest primary productivity, as the white-water seasonal flooding fertilizes *várzea* soils (Haugaasen and Peres, 2006). Higher abundance/biomass in *várzea* forests due to the higher primary productivity has been documented mainly for mammals, but also for arboreal ant species (Pringle et al., 2019).

Butterflies are strongly associated with specific habitats at all life stages (Freitas et al., 2006) and are relatively sedentary in the larval stage, but are highly vagile in the adult phase and can have seasonal adaptations (phenological or migratory) to environmental changes (Diamond et al., 2011; Chowdhury et al., 2021). Vegetation gradients represent changes in the availability of food resources and physical conditions of the environment, which directly affect the spatial distribution of Amazonian fruit-feeding butterflies (Ribeiro and Freitas, 2012; Graça et al., 2015, 2017a). Therefore, environmental changes, such as seasonal flooding, can also filter species from the regional pool, affecting local species richness and composition.

This study compares the butterfly assemblages of *várzea* and *terra firme* forests in central Amazonia. Specifically, we aim (i) to test whether the density, richness and composition of butterflies differs between *várzea* and *terra firme* forests; (ii) to compare the species-abundance distribution between the two forest types; and (iii) to evaluate how the assemblage structure is associated with environmental (topography and vegetation) gradients between and within forest types. We expected to find a higher butterfly density in *várzea* forests because they have higher forest primary productivity, which represents higher availability of food resources than in *terra firme* forests. On the other hand, given that *terra firme* forests represent a more stable environment and cover a larger area, we expected higher species richness in

this forest type. We also predicted that the species-abundance distribution would be even in *terra firme* forests due to its higher species richness, in comparison with *várzea* forests, in which we should find a higher dominance of abundant species. We also expected to find strong turnover in species composition associated with forest type and environmental gradients.

## MATERIALS AND METHODS

### Study Area

Sampling was undertaken in three Amazonian protected areas: Amanã Sustainable Development Reserve, Mamirauá Sustainable Development Reserve and Baixo Juruá Extractive Reserve, in the Middle-Solimões (upper Amazon) River region, in Central Amazonia (Figure 1). These protected areas contain floodplains covered largely by *várzea* forests, which are adjacent to *terra firme* forests (ICMBio, 2009; IDSMS, 2010). During the high-water season, *várzea* forests are flooded by nutrient-rich white-water rivers, with an average annual water-level range of 15 m. Highest river levels occur around May–June and minima in October–November (ICMBio, 2009; IDSMS, 2010). Mean annual temperature and precipitation were around 26–31°C and 2,200–2,400 mm, respectively, with mean precipitation around 60–80 mm during the dry season (ICMBio, 2009; IDSMS, 2010).

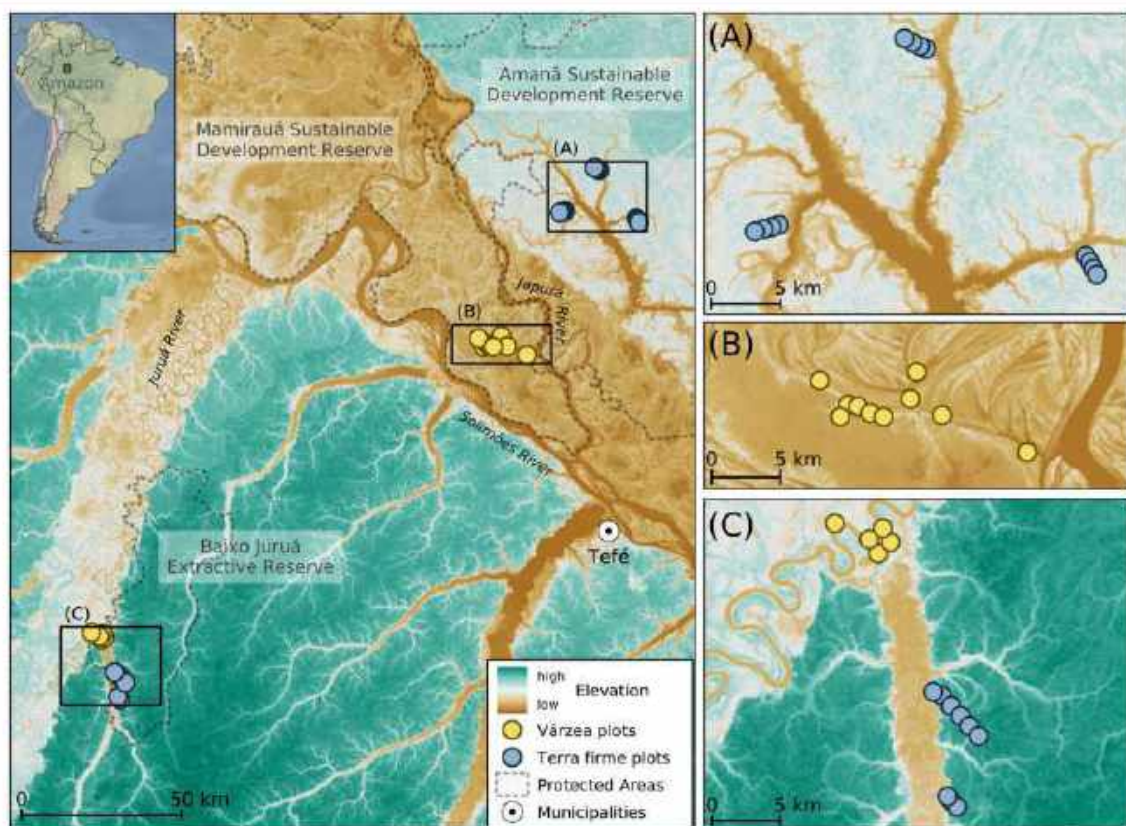
### Sampling Design and Data Collection

Sampling was done in 15 plots located in *várzea* and 21 in *terra firme* forests (Figure 1) during the low-water season in all study areas (RDS Amanã in November–December 2017, RESEX Baixo Juruá in July 2018, RDS Mamirauá in August 2019). We were not able to conduct sampling in both high- and low-water seasons due to logistical constraints. The sampling design followed the RAPELD method as part of a long-term ecological project that aims to compare the distributions of multiple taxa (Magnusson et al., 2005). Plots (sample units) consisted of a 250-m long center line, separated by at least 500 m from one another (Figure 1).

Butterfly surveys were conducted via active and passive sampling. We placed six equally spaced baited butterfly traps along the center line of each plot. Traps were hung from tree branches in the forest understorey (~1.5 m high). We baited the traps with a mixture of sugar-cane juice and bananas fermented for 48 h (Freitas et al., 2014) and visited them every 24 h to check for captures and replace the bait. We left the traps active for six consecutive days in each plot. This sampling effort is based on Graça et al. (2017b), who suggested that it is sufficient to identify ecological responses of understorey fruit-feeding butterfly assemblages.

We also used insect nets to sample low-flying Haeterini species and other Nymphalid species that usually are not caught with baited traps. On each visit to the plots, two researchers with standard 37-cm diameter insect nets actively searched for butterflies during 30 min. All captured individuals were collected for posterior species identification. Butterflies were identified to species level using on line resources<sup>1</sup> and the taxonomic literature. All identifications were verified by an

<sup>1</sup>www.butterfliesofamerica.com



**FIGURE 1** | Distribution of sample plots in várzea and terra firme forests. Maps show the distribution of sampling plots overlapped with an elevation Radar image from the Shuttle Radar Topography Mission (SRTM). Black rectangles in the left map are enlarged in right panels (A–C).

expert taxonomist (T. Zacca). To avoid taxonomic uncertainty, especially because our study area is located in a region with many biodiversity-knowledge shortfalls (Hortal et al., 2015), where butterflies have been poorly inventoried (Santos et al., 2008), some specimens could not be identified to species level, so we identified them as morphospecies. Although not ideal, the use of morphospecies is a way to deal with taxonomic constraints in ecological studies, and they appear to provide a reliable alternative to taxonomic species in Lepidoptera (91% of matching accuracy; Derraik et al., 2002). All specimens were deposited in the Entomological Collection of the Mamirauá Institute for Sustainable Development, Tefé, Brazil.

We gathered topographic and vegetation data to characterize the environmental gradients across *várzea* and *terra firme* plots. Topography data consisted of elevation, height above nearest drainage (HAND) and flooded terrain during the high-water season, which were extracted from an image provided by the Synthetic Aperture Radar of the Japanese Earth Resources Satellite—JERS-1 SAR.<sup>2</sup> In the Amazon, JERS-1/SAR images indicate flooded-forest areas by brighter pixels, closed-canopy forests by median brightness, and open water as darker pixels. Vegetation data consisted of estimates of % of tree cover, canopy height, enhanced vegetation index (EVI) and

net primary productivity (NPP) obtained from GIS databases (Supplementary Table 1). EVI is a vegetation index that is correlated with forest primary productivity and vegetation structure (Huete et al., 2002).

## Data Analysis

We report two indices of butterfly diversity: species density and rarefied species richness. These measures emphasize different components of diversity while controlling for potential sampling bias. Species density records the number of species per sample unit. The rarefied species richness (hereafter “species richness”), is used to estimate expected species richness at constant total abundance, since increased number of species is expected as a random consequence of larger pools of individuals (Gotelli and Colwell, 2001).

We compared the total abundance and observed number of species per plot between *várzea* and *terra firme* forests with Kruskal-Wallis tests, as the data had non-normal distributions. We used rarefaction and extrapolation of standardized number of species to compare species richness in both forest types. We standardized the number of species by both number of sampled individuals and sampling coverage, following the recommendations of Chao et al. (2014). Rarefaction and extrapolation were based on sampling coverage, in

<sup>2</sup><http://earth.esa.int>

addition to sample size, because standardizing samples by number of individuals usually underestimates species richness of assemblages with more species (Chao and Jost, 2012). We also used Kolmogorov-Smirnov tests to compare the species-abundance curves from the two forest types and sampling methods.

We built a species by site matrix, recording each species abundance (columns) per plot (rows). Then we standardized the abundances by dividing the number in each matrix cell by the total abundance in the matrix row (plots) to reduce the discrepancy between sites with different number of samples. We summarized butterfly species composition by non-metric multidimensional scaling (NMDS) ordination with two axes, based on the Bray-Curtis dissimilarity index. Then, we used a permutational multivariate analysis of variance (PERMANOVA) to evaluate whether the species composition differed between the two forest types. We reran this analysis excluding singletons and doubletons, since rare species can introduce variation in the assemblage structure that may not be related to habitat (Beja et al., 2010). We used a principal component analysis (PCA) to summarize the environmental data from plots and used the first axis of this ordination to represent the environmental gradient across plots. We then used an NMDS with one dimension to reduce the dimensionality of data into only one axis, using the scores derived from this ordination to represent the butterfly species composition in each plot. We used this second NMDS ordination with only one axis because NMDS is not an eigenvalue technique, and it does not maximize the variability associated with individual axes of the ordination, so the axes are not orthogonal to each other (Legendre and Legendre, 1998). We then used the single NMDS axis, which represented the ordering of sites according to their similarity in species composition (i.e., the assemblage structure), as the response variable in a generalized linear model (GLM) to evaluate whether it changes with environmental gradients (PCA 1) and across forest types (*várzea* or *terra firme*). We included latitude and longitude as predictors in the GLM to account for potential effect of spatial gradients and tested for spatial autocorrelation in model residuals with Moran's I. All analyses were undertaken in the *vegan* 2.4-4 (Oksanen et al., 2013) and *iNEXT* (Hsieh et al., 2016) packages of the R 3.4.4 statistical software (R Development Core Team, 2018).

## RESULTS

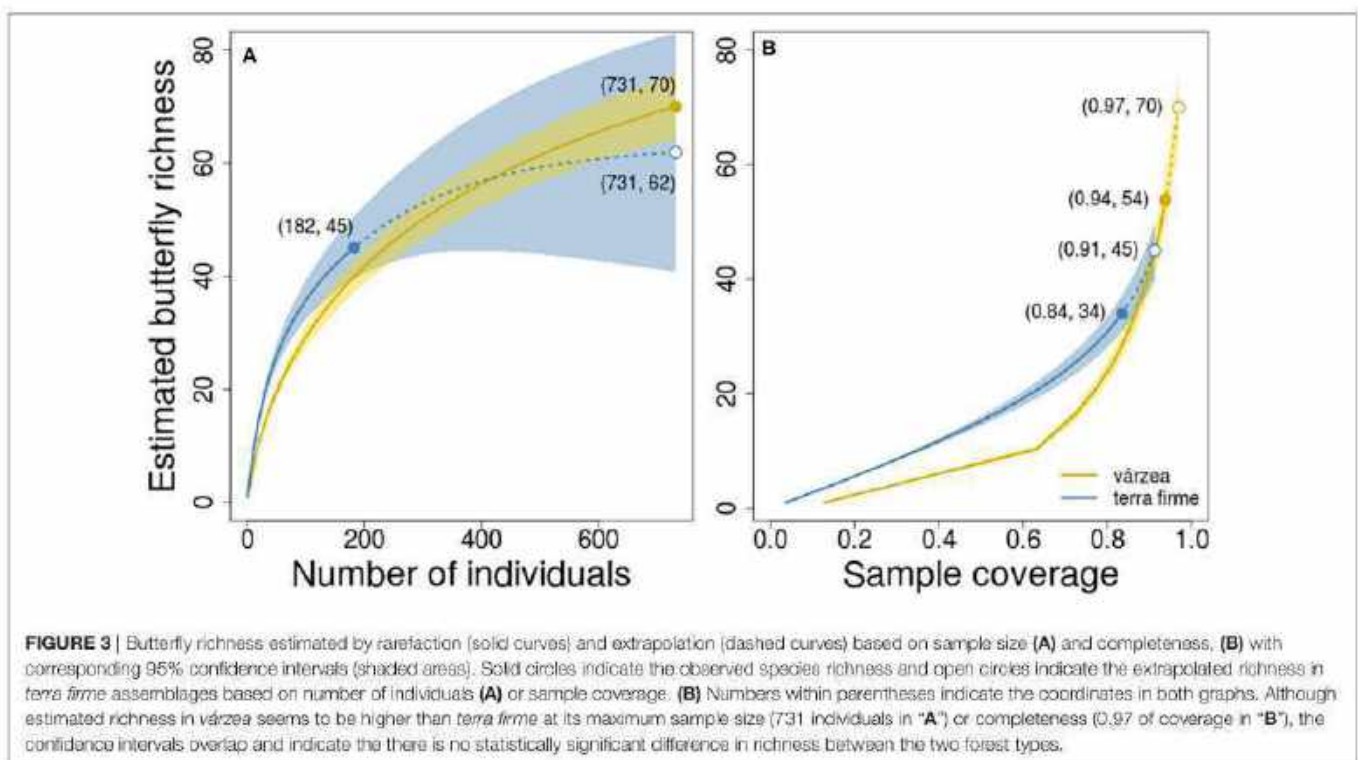
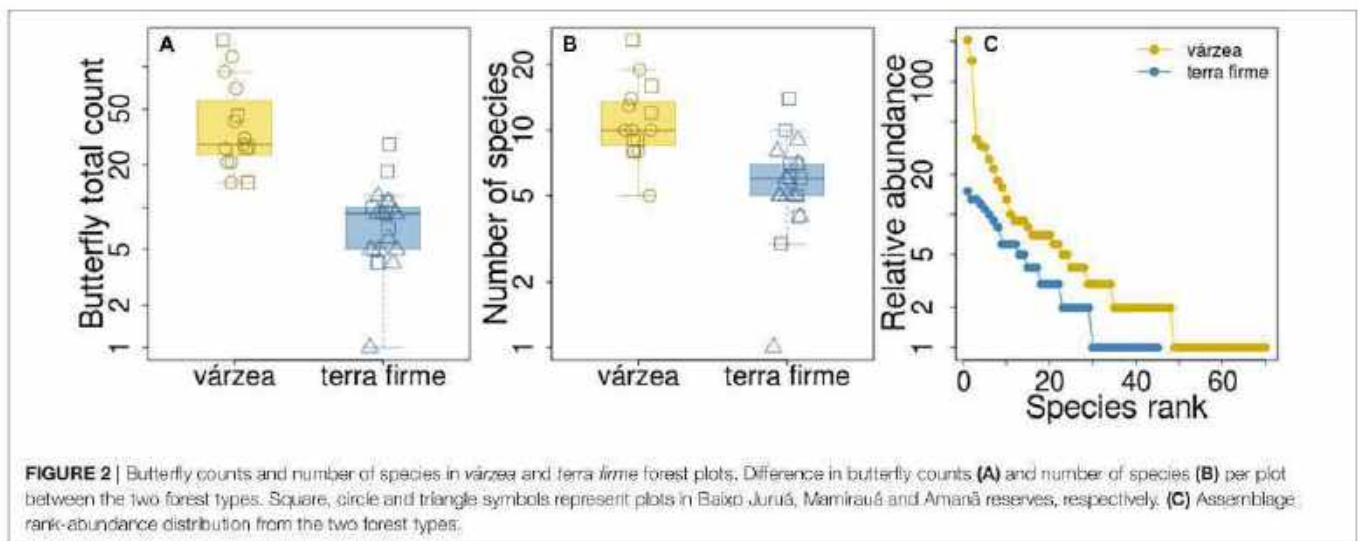
We captured 913 individuals belonging to 99 butterfly species (Supplementary Table 2), in a total sampling effort of 1,296 trap\*days (540 in *várzea* and 756 in *terra firme*) and 144 h (60 in *várzea* and 84 in *terra firme*). The most frequently captured species in *várzea* forests was *Magneptychia* aff. *ocnus*, whereas *Bia actorion* was the most frequently captured species in *terra firme* (Supplementary Figure 1). Singletons and doubletons were represented by 36 species (~51%) in *várzea* forests and 23 species (~51%) in *terra firme*. The number of species exclusive to *várzea* and to *terra firme* was 56 and 29, respectively, and 16 species were shared between the two forest types.

The median number of butterfly individuals counted per plot in *várzea* forests was 28 (first quartile (Q1) and third quartile (Q3) = 24 and 58, respectively), and it was significantly higher than the number of individuals counted in *terra firme* plots (Q1 = 5; median = 9; Q3 = 10; Kruskal-Wallis,  $H = 22.64$ ,  $p < 0.001$ ; Figure 2A). The abundance distribution of species also differed between the two forest types (Kolmogorov-Smirnov, baited traps:  $D = 0.85$ ,  $p < 0.001$ ; insect nets:  $D = 0.71$ ,  $p < 0.001$ ; both methods:  $D = 0.66$ ,  $p < 0.001$ ; Figure 2C and Supplementary Figure 2). The *várzea* assemblage had higher dominance of abundant species [three (4%) species made up 50% of all individuals, Supplementary Figure 1] than the *terra firme* assemblage, which had an even distribution of species abundance [eight (18%) species accounted for 50% of individuals, Supplementary Figure 1].

The observed number of species per plot was also higher in *várzea* than in *terra firme* forests (Kruskal-Wallis,  $H = 15.26$ ,  $p < 0.001$ ; Figure 2B), with a median number of 9 species per plot in *várzea* forests (Q1 = 9; Q3 = 14) and 6 (Q1 = 5; Q3 = 7) species per plot in *terra firme* forests. However, when the species richness estimate was standardized by sample size and coverage, *várzea* and *terra firme* forests showed similar species-richness estimates (Figure 3). *Terra firme* assemblages had a lower estimated sampling completeness (84%) than *várzea* (94%; Supplementary Figure 3), despite the larger survey effort (21 surveyed plots in *terra firme* against 15 in *várzea*). Even with *terra firme* having a lower sampling completeness, the rarefaction and extrapolation of species-richness to the same number of individuals or coverage as the *várzea* samples showed similar curves (Figure 3), indicating that they have similar overall richness.

The NMDS ordination of plots along the two axes explained 53% of the variation in differences in species composition, whereas the NMDS with a single axis explained 33%. The PCA ordination of plots along the first two axes explained 66% of the variation in the environmental features of plots and the first axis (PCA 1) captured the environmental differences between *várzea* and *terra firme* plots (Supplementary Figure 4). Negative values of the first PCA axis were associated with *várzea* plots, whereas positive values were associated with *terra firme* plots (Supplementary Figure 4). *Várzea* plots had lower terrain elevation, were vertically nearer to drainage, subjected to flooding during the high-water season, and also had lower percentage tree cover and lower canopy height than *terra firme* plots (Supplementary Figure 4).

There was a marked difference between butterfly composition of *várzea* and *terra firme* forests (PERMANOVA,  $F = 7.82$ ,  $p < 0.001$ ), captured mainly by the first axis (Figure 4A) due to the strong turnover of species composition between forest types (Figure 4B). The exclusion of rare species (singletons and doubletons) did not change the pattern found (Supplementary Figure 5). The change in species composition was associated with forest types ( $t = -4.59$ ;  $p < 0.001$ ), but with little evidence for effects of environmental gradients within each forest type (*várzea*:  $t = 0.09$ ;  $p = 0.93$ ; *terra firme*:  $t = -0.07$ ;  $p = 0.94$ ; Figure 4C), after controlling for spatial effects of latitude and longitude.



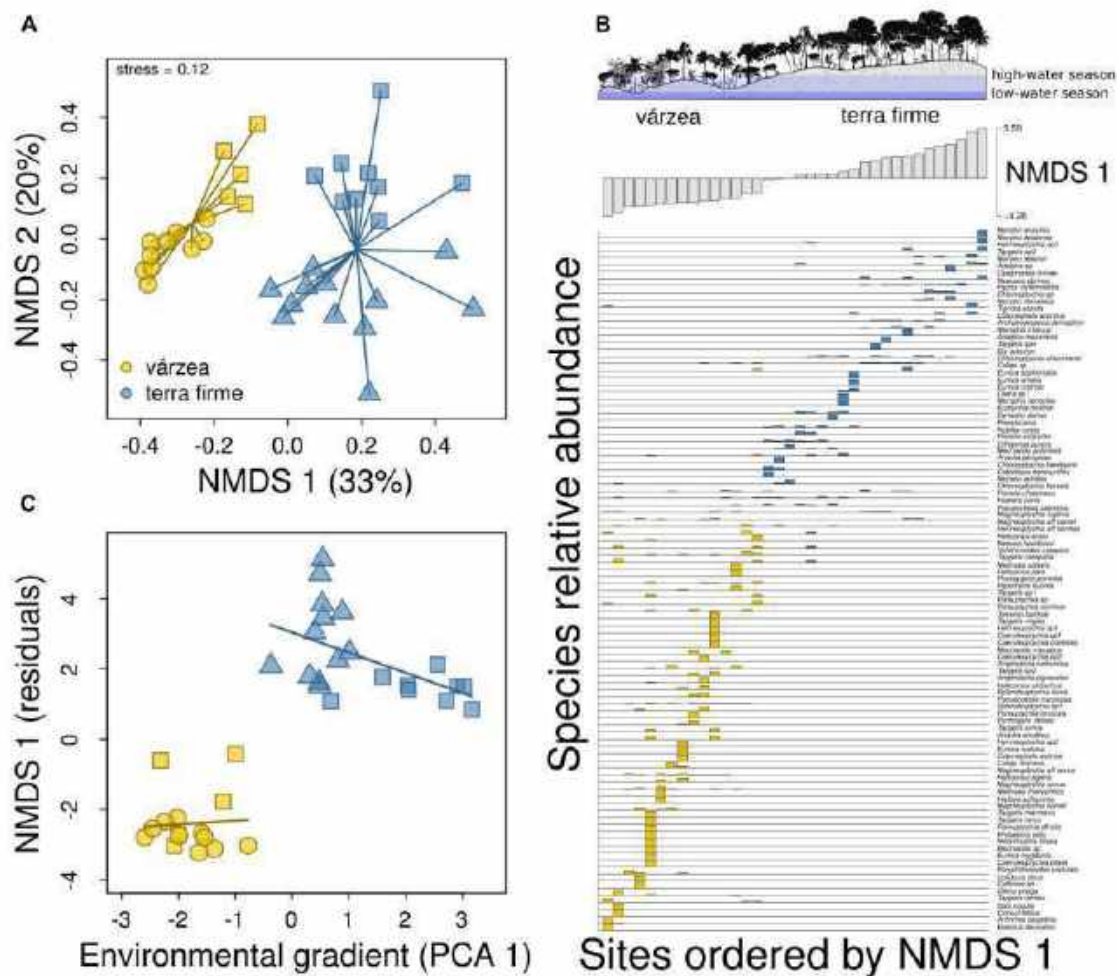
There was no spatial autocorrelation in model residuals (Moran's I: obs.: -0.01; exp.: -0.03;  $p = 0.60$ ), even without including latitude and longitude among predictors (Moran's I: obs.: -0.07; exp.: -0.03;  $p = 0.13$ ).

## DISCUSSION

### Bottom-Up Effects on Species Abundance and Richness

We found higher butterfly total abundance in *várzea* than in *terra firme* forests, which is the same pattern reported in studies

of bats (Pereira et al., 2009) and primates (Haugaasen and Peres, 2005b). The higher abundance of herbivorous, frugivorous and nectarivorous species (such as butterflies, primates and frugivorous bats) in *várzea* is probably due to the higher availability of food resources for these species in these forests. Seasonal flooding by white-water rivers provides an extra input of nutrients in *várzea* soils, which increases forest primary productivity (Irion et al., 2010). Bobrowiec et al. (2014) found that the abundance of frugivorous bats in *várzea* forests is even higher during the high-water season. However, for Amazonian fruit-feeding butterflies, adults tend to be more abundant during the early and mid-dry seasons, and less abundant during the wet



**FIGURE 4 |** Changes in species composition between *várzea* and *terra firme* forests. **(A)** Butterfly species composition in a bi-plot with the two axes derived from a NMDS ordination. Each point in the graph represents a plot located in *várzea* or *terra firme* forest and the distance between points represents the similarity of plots in terms of their species composition. Square, circle, and triangle symbols represent plots in Babo Juruá, Mamirauá, and Amaná reserves, respectively. **(B)** Distribution of butterflies across sample sites. Sample sites are ordered by a single NMDS axis and bar heights show the relative abundance of butterfly species across *várzea* (gray) and *terra firme* (black) plots. **(C)** Change in species composition (NMDS 1) with environmental gradients (PCA 1) along and within each forest type, after controlling for the effects of latitude and longitude.

season (Barlow et al., 2007), when they probably occur in other life stages, such as herbivorous caterpillars.

We found that *várzea* forests also had higher species density (i.e., higher numbers of species per plot) than *terra firme*. This apparent difference in the number of butterfly species between the two forest types occurred because we sampled a much higher number of individuals per plot in *várzea* forest. When extrapolating the *terra firme* species richness to the same number of individuals/coverage as the *várzea* sample, the assemblages showed similar overall richness, even though *terra firme* covers a larger area, has more stratified forest structure and is much older than *várzea* forests. A similar species richness between flooded and unflooded forests was also found for arboreal ants (Pringle et al., 2019). Empirical experiments with arboreal arthropods demonstrated that bottom-up mechanisms in which long-term higher input of nutrients increases species density, but slightly

decreases the richness of detritivores and herbivores due to increased dominance of common species (Haddad et al., 2000; Gruner and Taylor, 2006). This bottom-up process may explain why we found a higher species density, but not necessarily richness in *várzea* forests.

Previous studies have consistently found poorer assemblages in *várzea* forests for several animal groups (Haugaasen and Peres, 2005b; Bobrowiec et al., 2014; Alvarenga et al., 2018), including a recent study with butterflies (Oliveira et al., 2021). However, most of these studies reported only the species density (i.e., number of species per sampling unit) as a diversity index, and few attempted to estimate species richness by standardizing the number of species by sample size/coverage prior to undertaking such comparisons (but see Pereira et al., 2009; Oliveira et al., 2021). Therefore, the generalization of this pattern was likely based on species density (i.e., number of species per unit habitat),

which is different from rarefied (or expected) species richness at constant total abundance (Gotelli and Colwell, 2001).

However, Oliveira et al. (2021) did estimate butterfly species richness as we did, but found higher species richness in *terra firme* forests than in *várzea*. Although our sampling design is different from theirs, which hampers comparisons between studies, there are possible reasons for this difference. One is that they sampled not only Nymphalidae species, but also five other families of butterflies, which increases the overall diversity evaluated. Also, as these authors acknowledge, their limited sample size may have affected their species-accumulation curves, which did not approach an asymptote, so comparisons between curves may have been compromised.

## Environmental Filters and Adaptive Species Traits

Butterfly species composition changed with environmental gradients between forest types, but no effect of environmental gradients was detected within each forest type. It is likely that we did not detect the effects of environmental gradients within forest types because our measures of environmental variables were retrieved from GIS databases. Therefore, we caution that measuring micro-habitat characteristics in the field may be more appropriate to evaluate how assemblage structure responds to environmental gradients within each forest type.

On the other hand, species composition changed between *várzea* and *terra firme* forests. According to our PCA ordination, *várzea* forests are located at lower elevations nearer rivers, which causes inundation during the high-water season, and have lower tree cover and canopy height, whereas *terra firme* has a more complex forest structure and does not flood. The differences in butterfly species composition is probably mainly attributable to flooding, which is a direct barrier to the persistence of all ground-dwelling and understorey species during the high-water season (Haugaasen and Peres, 2005a), and even for flying species (birds, Beja et al., 2010; bats, Bobrowiec et al., 2014), such as butterflies.

We also found that *terra firme* assemblages from different protected areas had distinct butterfly composition (see separation of symbols captured by NMDS 2 in Figure 4A). We do not believe that these differences are due to an effect of the spatial distance between these assemblages, since we have controlled for potential effects of geographical distance and did not find spatial autocorrelation. While *terra firme* plots from Baixo Juruá Reserve are located in a region with very old soils from Tertiary sandstones, plots from Amanã Reserve are located on more recent soils from Late-Pleistocene, or *paleo-várzea* forests, as they have been called (Irion et al., 2010). Even so, *paleo-várzeas* are more similar to *terra firme* than to *várzea* in terms of topography and vegetation structure (taller and more stratified forests). As shown by the PCA ordination, these upland plots have distinct environmental conditions, depending on the geological formation in which they are located. Therefore, we believe that the distinct butterfly compositions among *terra firme* plots are probably due such environmental differences among study sites.

Habitat conditions may select for the evolution of adaptive traits and behavior, which in turn may affect the ability of

species to disperse to and persist at local sites. For example, the evenness rank-abundance distribution in *terra firme* forests had a considerable contribution from Haeterini butterflies, which tended to be more abundant in this forest type. Haeterini butterflies are low-flying ground-dwelling species that feed mainly on rotting fruits and other decaying material on the forest floor (Alexander and DeVries, 2012), and adults can be abundant throughout the year (Devries et al., 2012). Wing morphology in Haeterini butterflies has evolved as a response to their habitat-specific flight behavior, i.e., gliding in-ground along the forest floor (Cespedes et al., 2015). Therefore, it is possible that the adaptive wing shape traits of these species play an important role in constraining their dispersal through flooded forests.

Similarly, adaptive behavior may help to explain the larger abundance and richness of Ithomiini species in *várzea* forests. Ithomines commonly form large aggregations, also known as ithomine “pockets” (DeVries, 1987). This gregarious behavior normally occurs during the dry season, when temperatures are higher and air humidity is lower, so the pockets are located in shady forest sites close to water courses (Pinheiro et al., 2008). This adaptive behavior as a response to cope with adverse climate conditions was suggested to be the main factor explaining the formation of the pockets, rather than the occurrence of large concentrations of adult food resources (Pinheiro et al., 2008). Therefore, since most of the ithomine individuals were found in a few *várzea* plots located near the river banks (~70 m) and very close to small streams, it is likely that the higher abundance of ithomines in *várzea* forests is an adaptation of these butterflies to seek suitable local climatic conditions.

## The Role of Biotic Filters

The differences in species composition between the two forest types may also be explained by species interactions, especially with their host plants. For instance, the most frequently captured species in *várzea* assemblages were *Magneptychia* aff. *ocnus*, *Pseudodebis marpessa*, and *P. valentina*. Larvae of *Magneptychia* species feed mainly on grasses (Beccaloni et al., 2008), which have high growth rates and rapidly occupy available substratum during the low-water season in *várzea* forests (Silva et al., 2013). *Pseudodebis* species feed on the bamboo *Guadua angustifolia* (Murray, 2001), which was highly abundant in the *várzea* plots where we surveyed most *Pseudodebis* butterflies (Rabelo, person. obs.). On the other hand, *Bia actorion* and *Euptychia molina* were the most frequently captured species in the *terra firme* assemblages. *Bia actorion* feeds mainly on *Geonoma* palms (Freitas et al., 2002), which are considered *terra firme* specialists and rarely occur in *várzea* forests (Muscarella et al., 2019). Similarly, *Euptychia* butterflies are known for their strong relationship with their host plants, Selaginellaceae and Neckeraceae (DeVries, 1985; Hamm and Fordyce, 2016), which are often obligate terrestrial (*Selaginella*) and do not occur in floodplain forests (Poulsen and Balslev, 1991; Junk and Piedade, 1993). As most tropical caterpillars are host specialists and floristic diversity is closely associated with butterfly richness (Moraes et al., 2011) and composition (Graça et al., 2015), the distribution of host plants is the primary biotic limitation affecting butterfly composition at local scales.

Another interesting example of how biotic interactions may explain our results can be seen in the Onega clearwing (*Oleria onega*). This species was the fourth most common species in *várzea* forests. *Oleria* are Ithomiini butterflies that are known to feed on alkaloid-rich host plants, which make the adults unpalatable to predators and all species are engaged in mimicry (Brown, 1987; Beccaloni, 1997). Although adults are unpalatable, it has been suggested that their eggs may be subject to predation or removed from leaves by *Ectatomma* ants, which are often found in *Solanum* species (Gallusser, 2002). As *Ectatomma* ants are weak swimmers (Yanoviak and Frederick, 2014) and do not normally occur in Amazonian seasonally flooded forests (Wilson, 1987), we hypothesize that their absence may favor the high abundance of *Oleria* in *várzea* forests.

## CONCLUSION

We found that both *várzea* and *terra firme* forests have similar species richness, although the former forest type had higher species density likely due to its higher primary productivity. We also found a pronounced difference in butterfly species composition between *várzea* and *terra firme* forests. The strong turnover of butterfly species was associated with environmental differences between *várzea* and *terra firme*, but not with the environmental change within each forest type. Environmental conditions may select for the evolution of adaptive traits and behavior, which in turn may affect the ability of species to disperse to and persist at local sites. Therefore, our findings reinforce flooding as a primary environmental filter in Amazonian floodplain forests, which strongly determines the composition of butterfly assemblages, as well as the distribution of their interacting biota. The results of this study suggest that environmental and biotic filters override the effects of vegetation stratification and effects of source area on differences in the composition of butterfly assemblages in flooded and unflooded Amazonian sites at local scales.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the KNB Ecoinformatics repository (<https://knb.ecoinformatics.org/view/doi:10.5063/B27SQT>).

## ETHICS STATEMENT

The study and collection of butterfly specimens was reviewed and approved by the Sistema de Autorização e Informação

em Biodiversidade (SISBIO), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio; permission #57444).

## AUTHOR CONTRIBUTIONS

RR conceived and designed the study, collected and analyzed the data, and prepared the first draft of the manuscript. GP contributed to the study design, collected the data, and contributed to the manuscript preparation. JV contributed to the idea conception, study design, and manuscript preparation. WM contributed to study design, data analyses, and the manuscript preparation. All authors contributed to the article preparation and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.693178/full#supplementary-material>

## REFERENCES

- Alexander, L. G., and DeVries, P. J. (2012). Variation in capture height and trap persistence among three Costa Rican understory butterfly species. *J. Trop. Ecol.* 28, 585–589. doi: 10.1017/S0266467412000533
- Alvarenga, G. C., Ramalho, E. E., Baccaro, F. B., Rocha, D. G., Ferreira-Ferreira, J., and Dineeli Bobrowiec, P. E. (2018). Spatial patterns of medium and large size mammal assemblages in *várzea* and *terra firme* forests, Central Amazonia, Brazil. *PLoS One* 13:e0198120. doi: 10.1371/journal.pone.0198120
- Barlow, J., Overal, W. L., Araújo, I. S., Gardner, T. A., and Peres, C. A. (2007). The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *J. Appl. Ecol.* 44, 1001–1012. doi: 10.1111/j.1365-2664.2007.01347.x

- Beccaloni, G. W. (1997). Ecology, natural history and behaviour of Ithomiine butterflies and their mimics in Ecuador (LEPIDOPTERA: Nymphalidae: Ithomiinae). *Trop. Lepid.* 8, 103–124.
- Beccaloni, G. W., Viloria, A. L., Hall, S. K., and Robinson, G. S. (2008). *Catalogue of the Hostplants of the Neotropical Butterflies. Catálogo de las Plantas Huésped de las Mariposas Neotropicales*. Zaragoza: Sociedad Entomológica Aragonesa/Natural History Museum/Instituto Venezolano de Investigaciones.
- Beja, P., Santos, C. D., Santana, L., Pereira, M. J., Marques, J. T., Queiroz, H. L., et al. (2010). Seasonal patterns of spatial variation in understory bird assemblages across a mosaic of flooded and unflooded Amazonian forests. *Biodivers. Conserv.* 19, 129–152. doi: 10.1007/s10531-009-9711-6
- Bobrowiec, P. E. D., Rosa, L., do, S., Gazarini, J., and Haugaasen, T. (2014). Phyllostomid bat assemblage structure in amazonian flooded and unflooded forests. *Biotropica* 46, 312–321. doi: 10.1111/btp.12102
- Brown, K. S. Jr. (1987). Chemistry at the Solanaceae/Ithomiinae Interface. *Ann. Missouri Bot. Gard.* 74, 359–397. doi: 10.2307/2399406
- Céspedes, A., Penz, C. M., and DeVries, P. J. (2015). Cruising the rain forest floor: butterfly wing shape evolution and gliding in ground effect. *J. Anim. Ecol.* 84, 808–816. doi: 10.1111/1365-2656.12325
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., et al. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67. doi: 10.1890/13-0133.1
- Chao, A., and Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93, 2533–2547. doi: 10.1890/11-1952.1
- Chowdhury, S., Zalucki, M. P., Amano, T., Woodworth, B. K., Venegas-Li, R., and Fuller, R. A. (2021). Seasonal spatial dynamics of butterfly migration. *Ecol. Lett.* 24, 1814–1823. doi: 10.1111/ele.13787
- Derriak, J. G., Closs, G. P., Dickinson, K. J., Sirvid, P., Barratt, B. L., and Patrick, B. H. (2002). Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. *Conserv. Biol.* 16, 1015–1023. doi: 10.1046/j.1523-1739.2002.00358.x
- DeVries, P. J. (1985). Hostplants records and natural history notes on Costa Rican Butterflies (Papilionidae, Pieridae & Nymphalidae). *J. Res. Lepid.* 24, 290–333.
- DeVries, P. J. (1987). *The butterflies of Costa Rica and their Natural History Papilionidae, Pieridae, Nymphalidae*, Vol. I. New Jersey NJ: Princeton University Press.
- Devries, P. J., Alexander, L. G., Chacon, I. A., and Fordyce, J. A. (2012). Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *J. Anim. Ecol.* 81, 472–482. doi: 10.1111/j.1365-2656.2011.01922.x
- Diamond, S. E., Frame, A. M., Martin, R. A., and Buckley, L. B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology* 92, 1005–1012. doi: 10.1890/10-1594.1
- Freitas, A. V., Leal, I. R., Uehara-Prado, M., and Iannuzzi, L. (2006). "Insetos como indicadores de conservação da paisagem," in *Biologia da Conservação e Manejo da Vida Silvestre*, eds L. Cullen Jr., R. Rudran, and C. Valladares-Padua (Curitiba: Editora da Universidade Federal do Paraná), 357–384.
- Freitas, A. V. L., Iserhard, C. A., Santos, J. P., Carreira, J. Y. O., Ribeiro, D. B., Melo, D. H. A., et al. (2014). Studies with butterfly bait traps: an overview. *Rev. Colomb. Entomol.* 40, 203–212.
- Freitas, A. V. L., Murray, D., and Brown, J. S. (2002). Immatures, natural history and the systematic position of *Bia uctorion* (Nymphalidae). *J. Lepid. Soc.* 56, 117–122.
- Gallusser, S. A. (2002). *Biology, Behaviour and Taxonomy of Two Oleria Oneia Subspecies (Ithomiinae, Nymphalidae, Lepidoptera) in North-Eastern Peru*. Doctoral's Thesis. Neuchâtel: University of Neuchâtel.
- Gascon, C. (1996). Amphibian litter fauna and river barriers in flooded and non-flooded Amazonian rain forest. *Biotropica* 28, 136–140. doi: 10.2307/2388779
- Gotelli, N. J., and Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. doi: 10.1046/j.1461-0248.2001.00230.x
- Graça, M. B., Morais, J. W., Franklin, E., Pequeno, P. A. C. L., Souza, J. L. P., and Bueno, A. S. (2015). Combining taxonomic and functional approaches to unravel the spatial distribution of an amazonian butterfly community. *Environ. Entomol.* 45, 301–309. doi: 10.1093/ee/nvv183
- Graça, M. B., Pequeno, P. A. C. L., Franklin, E., Souza, J. L. P., and Morais, J. W. (2017a). Taxonomic, functional, and phylogenetic perspectives on butterfly spatial assembly in northern Amazonia. *Ecol. Entomol.* 42, 816–826. doi: 10.1111/een.12454
- Graça, M. B., Souza, J. L. P., Franklin, E., Morais, J. W., and Pequeno, P. A. C. L. (2017b). Sampling effort and common species: Optimizing surveys of understory fruit-feeding butterflies in the Central Amazon. *Ecol. Indic.* 73, 181–188. doi: 10.1016/j.ecolind.2016.09.040
- Gruner, D. S., and Taylor, A. D. (2006). Richness and species composition of arboreal arthropods affected by nutrients and predators: a press experiment. *Oecologia* 147, 714–724. doi: 10.1007/s00442-005-0337-4
- Haddad, N. M., Haarstad, J., and Tilman, D. (2000). The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* 124, 73–84. doi: 10.1007/s004420050026
- Hamm, C. A., and Fordyce, J. A. (2016). *Selaginella* and the satyr: euptychia westwoodi (Lepidoptera: Nymphalidae) oviposition preference and larval performance. *J. Insect Sci.* 16, 1–4. doi: 10.1093/jisesa/iwv018
- Haugaasen, T., and Peres, C. A. (2005a). Mammal assemblage structure in Amazonian flooded and unflooded forests. *J. Trop. Ecol.* 21, 133–145. doi: 10.1017/S026646740400207X
- Haugaasen, T., and Peres, C. A. (2005b). Primate assemblage structure in Amazonian flooded and unflooded forests. *Am. J. Primatol.* 67, 243–258. doi: 10.1007/s10329-009-0133-4
- Haugaasen, T., and Peres, C. A. (2006). Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. *Acta Amaz.* 36, 25–36. doi: 10.1590/s0044-59672006000100005
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., and Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Syst.* 46, 523–549. doi: 10.1146/annurev-ecolsys-112414-054400
- Hsieh, T. C., Ma, K. H., and Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. doi: 10.1111/2041-210X.12613
- Hubbell, S. P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* 19, 166–172. doi: 10.1111/j.0269-8463.2005.00965.x
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., and Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* 83, 195–213. doi: 10.1016/S0034-4257(02)00096-2
- ICMBio (2009). *Plano de Manejo – Reserva Extrativista do Baixo Jurua*. Tefe, AM: Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio / Ministério do Meio Ambiente.
- IDSMS (2010). *Plano de Gestão Reserva de Desenvolvimento Sustentável Mamirauá RDSM*. Tefe: MCTI/IDSMS-OS.
- Irion, G., Mello, J. A. S. N., Morais, J., Piedade, M. T. F., Junk, W. J., and Garimig, L. (2010). "Development of the amazon valley during the middle to late quaternary: sedimentological and climatological observations," in *Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, eds W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin (New York NY: Springer), 27–42. doi: 10.1007/978-90-481-8725-6\_2
- Junk, W. J., and Piedade, M. T. F. (1993). Herbaceous plants of the Amazon floodplain near Manaus: species diversity and adaptations to the flood pulse. *Amazoniana* 7, 467–484.
- Junk, W. J., Piedade, M. T. F., Schöngart, J., and Wittmann, F. (2012). A classification of major natural habitats of Amazonian white-water river floodplains. *Wetl. Ecol. Manag.* 20, 461–475. doi: 10.1007/s11273-012-9268-0
- Legendre, P., and Legendre, L. (1998). *Numerical Ecology*. Amsterdam: Elsevier.
- MacArthur, R. H. (1969). Patterns of communities in the tropics. *Biol. J. Linn. Soc.* 1, 19–30. doi: 10.1111/j.1095-8312.1969.tb01809.x
- MacArthur, R. H., and MacArthur, J. W. (1961). On bird species diversity. *Ecology* 42, 594–598.
- MacArthur, R. H., and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton NJ: Princeton University Press.
- Magnusson, W. E., Lima, A. P., Luizão, R., Luizão, F., Costa, F. R. C., Castilho, C. V., et al. (2005). RAPEL: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotrop.* 5, 21–26.

- Melack, J. M., and Hess, L. L. (2010). "Remote sensing of the distribution and extent of wetlands in the Amazon basin," in *Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Development*, eds W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin (New York NY: Springer), 43–59. doi: 10.1007/978-90-481-8725-6\_3
- Morais, H. C., Sujii, E. R., Almeida-Neto, M., De Carvalho, P. S., Hay, J. D., and Diniz, L. R. (2011). Host plant specialization and species turnover of caterpillars among hosts in the Brazilian Cerrado. *Biotropica* 43, 467–472. doi: 10.1111/j.1744-7429.2010.00736.x
- Murray, D. L. (2001). *Systematics of Neotropical Satyrine Butterflies (Nymphalidae: Satyrinae: Euphydryina) Based on Larval Morphology and DNA Sequence Data and the Evolution of Life History Traits*. Doctoral's Dissertation. Baton Rouge (LA): Louisiana State University.
- Muscarella, R., Bacon, C. D., Faurby, S., Antonelli, A., Kristiansen, S. M., Svenning, J. C., et al. (2019). Soil fertility and flood regime are correlated with phylogenetic structure of Amazonian palm communities. *Ann. Bot.* 123, 641–655. doi: 10.1093/aob/mcy196
- Oksanen, A. J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., Hara, R. B. O., et al. (2013). *vegan: Community Ecology Package*. R package version 2.0-10.
- Oliveira, I. F., Baccaro, F. B., Werneck, F. P., Zacca, T., and Haugaasen, T. (2021). Marked differences in butterfly assemblage composition between forest types in Central Amazonia. *Brazil. Forests* 12:942. doi: 10.3390/f12070942
- Pereira, M. J. R., Marques, J. T., Santana, J., Santos, C. D., Valsecchi, J., Queiroz, H. L., et al. (2009). Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. *J. Anim. Ecol.* 78, 1163–1171. doi: 10.1111/j.1365-2656.2009.01591.x
- Pinheiro, C. E. G., Medri, I. M., and Salcedo, A. K. M. (2008). Why do the Ithomiines (Lepidoptera, Nymphalidae) aggregate? Notes on a butterfly pocket in central Brazil. *Rev. Bras. Entomol.* 52, 610–614. doi: 10.1590/s0085-56262008000400012
- Poulsen, A. D., and Balslev, H. (1991). Abundance and cover of ground herbs in an Amazonian rain forest. *J. Veg. Sci.* 2, 315–322. doi: 10.2307/3235922
- Pringle, E. G., Santos, T. F. D., Gonçalves, M. S., Hawes, J. E., Peres, C. A., and Baccaro, F. B. (2019). Arboreal ant abundance tracks primary productivity in an Amazonian whitewater river system. *Ecosphere* 10:e02902.
- R Development Core Team (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ribeiro, D. B., and Freitas, A. V. L. (2012). The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon. *Brazil. J. Insect Conserv.* 16, 733–744. doi: 10.1007/s10841-012-9458-3
- Ruokolainen, K., Moullet, G. M., Zuquim, G., Hoorn, C., and Tuomisto, H. (2018). river network rearrangements in amazonia shake biogeography and civil security. *Preprints* 1–16. doi: 10.20944/preprints201809.0168.v1
- Santos, E. C., Mielke, O. H. H., and Casagrande, M. M. (2008). Butterfly inventories in Brazil: the state of the art and the priority-areas model for research aiming at conservation. *Nat. Conserv.* 6, 178–200.
- Silva, T. S. F., Melack, J. M., and Novo, E. M. L. M. (2013). Responses of aquatic macrophyte cover and productivity to flooding variability on the Amazon floodplain. *Glob. Chang. Biol.* 19, 3379–3389. doi: 10.1111/gcb.12308
- Wilson, E. O. (1987). The arboreal ant fauna of peruvian amazon forests: a first assessment. *Biotropica* 19, 245–251. doi: 10.2307/2388342
- Wittmann, F., Junk, W. J., and Piedade, M. T. F. (2004). The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *For. Ecol. Manage.* 196, 199–212. doi: 10.1016/j.foreco.2004.02.060
- Yanoviak, S. P., and Frederick, D. N. (2014). Water surface locomotion in tropical canopy ants. *J. Exp. Biol.* 217, 2163–2170. doi: 10.1242/jeb.101600

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### Capítulo III.

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Rabelo, R.M.; Dambros, C.; Graça, M.B.C.S.; Pereira, G.C.N.; Oliveira, I.F.; Plaza, T.G.D.; Valsecchi, J.; Magnusson, W.E. **The relative role of environment and dispersal as drivers of Amazonian fruit-feeding-butterfly distributions.** Manuscrito em preparação para *Ecography*.

## ORIGINAL RESEARCH

### **The relative role of environment and dispersal as drivers of Amazonian fruit-feeding-butterfly distributions**

Rafael M. Rabelo, Cristian Dambros, Márlon B. C. S. Graça, Geanne C. N. Pereira, Isabela F. Oliveira, Tarik Godoy Dangl Plaza, João Valsecchi, William E. Magnusson

#### **ABSTRACT**

There has been intensive debate on the role of environmental and dispersal limitation in explaining the composition of Amazonian species, without a clear consensus on which factors are more important at which spatial scales. Here, we investigate how butterfly species richness and composition are associated with spatial predictors, biogeographical regions delimited by rivers and environmental gradients at broad geographic scales in Amazonia. We surveyed fruit-feeding butterflies in 148 sample plots across the Brazilian Amazon. Plots covered an area of 730,000 km<sup>2</sup> and encompassed five major biogeographic regions delimited by Amazonian rivers. Environmental variables (climate, vegetation and soil) were obtained from GIS databases. Butterfly species richness increased with solar radiation, temperature, rainfall, distance from the Equator and from East to West. Environmental gradients, especially climatic, are strongly associated with butterfly turnover, which suggests that species are specialized to different parts of the environmental gradients (i.e., niche partitioning). The effects of geographic position/distance tended to be less important, suggesting that butterflies are less likely to be limited by dispersal at broad scales. The effect of river barriers likely results from a combination of factors, due to the correlation between environmental conditions and areas of endemism limited by rivers, which are also naturally spatially-structured. Our findings suggest that environmental conditions are more important than dispersal limitation (isolation by distance or river barriers) to explain the variation in Amazonian butterfly assemblages at broad scales.

## INTRODUCTION

Spatial distributions of species are often limited by dispersal ability, environmental constraints and biotic interactions. These factors may act, together or separately, to influence species distributions at different spatial scales. At wider geographic scales, the spatial distribution of species is the result of synergistic effects of dispersal limitation, which impedes species from occurring everywhere (Hubbell 2001, Warren et al. 2014), and environmental constraints, which results in patchy distributions of environmentally adapted species (Tuomisto et al. 2003). Although changes in species assemblages are frequently associated with geographical distance (e.g., Svenning et al. 2011) and environment (e.g., Hawkins et al. 2003), attributing the patterns to underlying dispersal or environmental processes is often challenging.

There has been a long debate on the role of environmental and dispersal limitation in explaining the composition of Amazonian species, without a clear consensus on which factors are more important at which spatial scales. In Amazonia, large rivers are the most obvious potential barriers to dispersal of terrestrial species, and they have been recognized as boundaries for distributions of several vertebrate groups (e.g., birds, Ribas et al. 2012; primates, Boubli et al. 2015; and lizards, Dias-Terceiro et al. 2015). The differences in species composition, especially for birds and primates, between opposite river banks has led to the classification of Amazonia into large interfluvial areas of endemism (Cracraft 1985; Da Silva et al. 2005; Naka 2011; Borges and Da Silva 2012; Fig. 1). However, for taxa with higher dispersal ability, geographical barriers, such as large rivers, are unlikely to limit species ranges (e.g., plants, Tuomisto et al. 2003; and insects, Penz et al. 2015, Dambros et al. 2017, Guilherme et al. 2021), which should be more strongly limited by environmental conditions. For that reason, there is controversy over the extent to which the association of species distribution boundaries with rivers is a pattern that can be generalized to a wide range of organisms (Santorelli et al. 2018).

Even in the absence of dispersal barriers, the distribution of a species may be limited by its dispersal ability, resulting in differences in species composition between sites (Hubbell 2001). Also, environmental factors, such as soil features and climate, are often spatially structured, which can also lead to differences in species composition due to environmental heterogeneity (Leibold and Mikkelsen 2002, Tuomisto et al. 2003,

Zuquim et al. 2012). Several studies have investigated the influence of river barriers and environmental heterogeneity for specific taxa (e.g., plants, Tuomisto et al. 2016; termites, Dambros et al., 2017; birds, Maximiano et al. 2020; ants, Guilherme et al. 2021) and for a broad range of taxonomic groups (Dambros et al. 2020), but reached different conclusions regarding the relative importance of these factors, depending on the taxonomic group evaluated.

Butterflies are abundant animals in tropical forests (Freitas et al. 2006). Environmental gradients, such as topography and vegetation structure, are expected to be strongly associated with species distributions at local scales (Ribeiro and Freitas 2012, Graça et al. 2015, Rabelo et al. 2021). On the other hand, climate was found to play an important role in determining the patterns of butterflies distribution at wider spatial scales (Menéndez et al. 2007, Stefanescu et al. 2011), but no detailed study has been conducted in the Amazon. Unlike many vertebrate species, butterflies can disperse quickly and over large distances (Penz et al. 2015). Although several genera are widely distributed, tropical forests harbor higher diversity (Legg 1978), which suggests that climate is likely to affect species distributions at wider scales.

We investigated how butterfly species richness and composition are associated with spatial predictors, biogeographical regions delimited by rivers and environmental gradients (climate, soil and vegetation) at broad geographic scales in Amazonia. We also quantified the relative contributions of geographical position, riverine barriers and environmental gradients to species turnover. We expected that species richness would be more strongly associated with environmental gradients than geographic predictors, and that richness would increase with temperature, precipitation and solar radiation. We also hypothesized that environmental variables, especially climate, may be more strongly associated with changes in species composition than geographic constraints and riverine barriers due to the high dispersal ability of butterfly species.

## **MATERIALS AND METHODS**

### *Sampling design and data collection*

Sampling covered a broad geographic scale across Amazonia (Fig. 1). This area encompasses a gradient of contrasting environmental variables (climate, vegetation and soils), as well as a gradient of geographical distances between sampling plots. We

surveyed butterflies between April 2011 and December 2019 in 148 sampling plots in 19 grids of five to 24 sampling plots each (Fig. 1). Grids and plots were established by researchers from the Brazilian Biodiversity Research Program (PPBio), a long-term ecological project that aims to compare the distribution of multiple taxa using standardized protocols (Magnusson et al. 2005). Plots (sample units) consisted of a 250-m long center line, separated by at least 500 m from one another. The distance between grids varied from dozens of kilometers to ~1910 km, and grids were spread over an area encompassing of about 730.000 km<sup>2</sup>. Most plots were located in tall, dense, lowland *terra-firme* tropical forests, but some were also placed in seasonally flooded *várzea* forests, and a few were established in cloud forests in the Guayana Highlands and white-sand forests with simpler vegetation structure (locally known as *Campinas* and *Campinaranas*).

Butterfly surveys were conducted via passive sampling with Van Someren-Rydon baiting traps. We placed from four to eight equally-spaced butterfly bait traps along each transect, hanging half of the traps in tree branches in the understorey (1.5 – 2 m high) and the other half in the canopy (15 – 20 m high). We baited the traps with a mixture of sugar-cane juice and bananas fermented for 48-h (Freitas et al. 2014) and checked them every 24 h to record captures and replace the bait. We left the traps active from five to eight consecutive days. All captured butterflies were collected for posterior identification and the specimens were deposited in the entomological collections of the National Institute of Amazonian Research, Mamirauá Sustainable Development Institute, University of São Paulo, and the Federal University of Rio Grande do Sul.

We gathered climatic, edaphic and vegetation data for every plot location from GIS online databases. We obtained data on two bioclimatic variables (mean annual temperature and annual precipitation) at ~1-km resolution from WorldClim version 2.1 (<http://www.worldclim.org>; Fick and Hijmans, 2017). We also converted WordClim monthly data of solar radiation from 1970 to 2000 into mean annual solar radiation. We used two variables of soil texture (percentage of sand and clay), which are related to soil drainage, obtained from SoilGrids database (<http://www.soilgrids.org>) at 250-m resolution. We also used one soil chemical variable related to nutrient availability (soil cation concentration), obtained from a modeled raster layer that uses both direct soil measures and estimates based on the occurrence of soil-indicator plant species (Zuquim

et al. 2019). To account for differences in vegetation structure, we obtained data on percentage of tree cover at 1-km resolution derived from the NOAA's Advanced Very High Resolution Radiometer data (AVHRR; <http://earthexplorer.usgs.gov>) and canopy height derived from spaceborne LiDAR and cloud-free MODIS at 500-m resolution (<https://daac.ornl.gov>; Sawada et al., 2015).

To test the relevance of Amazonian areas of endemism limited by rivers for the butterflies, we assigned each sampling plot to its corresponding area of endemism and used it as a predictor variable in subsequent analyses. We considered the currently accepted classification of Amazonian areas of endemism, which was initially proposed by Cracraft (1985) and subsequently modified by Da Silva, Novaes and Oren (2002), Naka (2011) and Borges and Da Silva (2012).

#### *Data analysis*

Before evaluating the effects of spatial and environmental variables on species richness and composition, we firstly investigated the multicollinearity among predictor variables based on the variance inflation factor (VIF) through a stepwise procedure, using a correlation threshold of 0.7 and a VIF threshold of 10 (Table S1). Mean annual solar radiation was highly correlated with latitude ( $r = 0.88$ ), so it was not included in subsequent regression models. As solar radiation is known to strongly affect butterfly distributions (Turner et al. 1987), we estimated its effects on species richness and composition by substituting the whole value of latitude for its module value to avoid collinearity problems, since these two variables were weakly correlated ( $r = -0.46$ ). All environmental and spatial variables were standardized before analyses to zero mean and unit variance.

We used the number of observed species per plot (estimate of species richness) as a response variable in a generalized linear model with Poisson distribution, using the environmental variables as predictor variables. We also included latitude and longitude among predictors to account for spatial gradients. All environmental and spatial variables were standardized before analyses to zero mean and unit variance. We compared models containing all possible combinations of predictor variables with the corrected Akaike Information Criterion (AICc). We finally determine the amount of variance in butterfly species richness associated with spatial and environmental factors using variance partitioning to separate the variation in species richness explained

uniquely by: (i) environmental variables (environment); (ii) latitude and longitude, possibly caused by neutral processes or variables that cause clumping not included in the analysis (“space”); (iii) both environment and “space” (environment + “space”); and (iv) unexplained variation not associated with clumping (residual).

To disentangle the relative roles of dispersal and environmental filters on species composition, we firstly used an occurrence species-site matrix in a Principal Coordinate Analysis (PCoA) based on the Jaccard dissimilarity index. The first PCoA axis was used to represent species composition in the multiple regression models, using spatial coordinates, environmental variables, and areas of endemism as predictor variables. It is virtually impossible to separate the effect of geographical coordinates and area of endemism in the raw-data approach, since biogeographic units are spatially structured. Therefore, we conducted those analyses using geographic position only or area of endemism only among predictors, each together with environmental variables. Environmental conditions among areas of endemism may also be spatially structured, so we performed a Principal Component Analysis (PCA) to investigate environmental differences among areas of endemism. We compared models with all possible combinations of predictor variables with the corrected Akaike Information Criterion (AICc) to select a plausible model and used the Moran’s I to calculate spatial autocorrelation of the residuals in the selected model. We also estimated the amount of variance in the first axis representing butterfly species composition associated with spatial coordinates, areas of endemism and environmental variables using variance partitioning. We finally tested for differences in species composition between pairs of areas of endemism using a posteriori Tukey test.

We followed the analytical approach used in Dambros et al. (2020) and also adopted a distance-based method to evaluate how geographical and environmental distances affect butterfly compositional similarity between sites. While raw-data method asks if the response variable varies directly in relation to predictors, distance-based method asks what determines the compositional dissimilarity between sampling plots: isolation by distance, by river barriers or by environmental differences. In this approach, the response variable was a pairwise dissimilarity matrix using 1-Jaccard index, in which the species composition of each site was compared with all others’, with cell values representing the degree of compositional dissimilarity between pairs of sites. Predictor

variables in were distance matrices quantifying the geographical distance and the degree of environmental difference between pairs of sites. Geographical distance values were logarithmically transformed prior to analysis to account for the tendency of lower distance decay at larger distances (Hubbel 2001; Tuomisto et al. 2003). We calculated the environmental-distance matrices based on Euclidean distances independently considering the whole set of environmental variables. Difference in the areas of endemism was defined as zero between plots embedded in the same area of endemism and one for plots located in different areas. We tested whether the species dissimilarity of plots was related to geographic distance, environmental difference, or separation by river barriers, using distance-based multiple regressions and variance partitioning. We tested for multicorrelation among distance matrices before running the model (Table S2). It should be noted that variances in distance models cannot be compared to variances in raw-data analyses, which have a physical interpretation. We did not test for normality in this model, since p-values calculated using permutation (i.e. a non-parametric test) do not assume normality in model residuals. All analyses were carried out in the R environment (R Development Core Team 2018) using ‘vegan’ (Oksanen et al. 2013) and ‘ecoDist’ (Goslee and Urban 2007) packages, as well as functions created to automate the process of running multiple regression models on distance matrices.

## RESULTS

We captured 2,700 individuals belonging to 189 species or morphospecies in the 148 sampled plots, in a total sampling effort of 717,340 trap\*days. The number of species per plot varied from 1 to 29, with median of 6 species per plot (first and third quartile were 4 and 9, respectively). Singletons and doubletons were represented by 42 (~22%) and 25 (~13%) species and species-accumulation curves did not approach an asymptote (Fig. S1).

### *Species richness*

The selected model for explaining species richness (Table S3) according to predictor variables explained 24% of the variation in species richness (Table 1). Butterfly species richness was higher in areas with higher solar radiation, temperature and precipitation (Table 1; Fig. 2). Species richness was also affected by longitude, reaching higher mean richness at western sample sites, but did not change significantly along latitude (Table

1). However, when considering the module of latitude in the model containing solar radiation as predictor, butterfly richness increased with distance from the Equator (Fig. S2). Despite the effects of spatial predictors, there was no spatial autocorrelation in model residuals (Moran's I: obs.: -0.003; exp.: -0.007;  $p = 0.52$ ), and environmental variables had the largest unique contribution to explain species richness (Table 1).

### *Species composition*

The PCoA ordination of plots along the first two axes explained 13% of the variation in species composition (PCoA 1 = 7%; PCoA 2 = 6%). Geographic position and environmental variables (except for temperature and soil cation concentration) showed a strong correlation with both PCoA axes (Fig. 3). Explanatory variables in the selected model explained 44% of the variation in the species composition summarized in PCoA 1 (Table 1). According to selected model (Table S4), butterfly species composition was associated with both environmental and spatial predictors (Table 1, Fig. 2). Model residuals did not show spatial structure (Moran's I: obs.: -0.0002; exp.: -0.007;  $p = 0.21$ ). However, we did not find clear differences in species composition among areas of endemism, except for the assemblages from the Guyana area of endemism, which presented distinct butterfly assemblages in comparison with other studied biogeographic areas (Fig. 3; Fig. S3). Guyana and Gran Sabana areas of endemism also presented clearly distinct environmental conditions in comparison with other biogeographic areas (Fig. S4). Variance partitioning showed that areas of endemism had the largest unique contribution to explain butterfly species turnover, followed by environmental predictors and geographic position (Table 1; Fig. 4).

There was a weak decay in species compositional similarity between sites with increasing geographical distance, but with several reversals of this general trend at some intervals of geographical distance (see splines in Fig. 5a). These changes in the main trend coincided with increases of environmental similarity with increasing geographical distance (Fig. 5c). Butterfly compositional similarity showed a clearer decreasing trend with increasing environmental distance, with no major reversals in the main trend (Fig. 5b). Environmental distance showed the strongest association with the decay in similarity ( $\beta = 0.27$ ;  $p = 0.01$ ), followed by geographical distance ( $\beta = 0.14$ ;  $p = 0.01$ ). Differences in areas of endemism did not show a significant association with compositional similarity between sites ( $\beta = 0.03$ ;  $p = 0.07$ ). Variance partitioning

showed that environmental distance had the largest unique contribution to explain the butterfly compositional similarity, whereas geographical distance and differences in area of endemism had very little importance (Fig. S5).

## DISCUSSION

### *The role of spatial and environmental factors*

We found that environmental factors, especially temperature, precipitation and solar radiation, are important drivers of butterfly species richness and composition. These findings are consistent with the expectation that species with higher dispersal capacity are more strongly affected by local environmental conditions (Hubbell 2005). Regional patterns of butterfly richness are often explained by climatic variables and richness tends to be higher in warm and humid regions (Hawkins and Porter 2003, White and Kerr 2006, Menéndez et al. 2007, Stefanescu et al. 2011), although, to the best of our knowledge, no study have investigated such broad-scale pattern in the Neotropics. Also, our findings are consistent with previous studies that showed the association of species turnover along environmental gradients in Amazonia (e.g., Tuomisto et al. 2003; Zuquim et al. 2012; Dias-Terceiro et al. 2015; Dambros et al. 2017; Fluck et al. 2020). Species turnover is a consequence of niche partitioning, in which species are specialized to different parts of the environmental gradient (Leibold and Mikkelsen 2002), and the relative importance of environment in shaping biological assemblages may depend on species ecological traits (De Bie et al. 2012). As ectothermic organisms, adult butterflies depend on warm temperatures and high solar radiation to maintain their normal activity (Turner et al. 1987). Therefore, warm temperatures and high solar radiation increase butterfly metabolic rates, which in turn may increase rates of genetic divergence and speciation, increasing overall diversity towards the tropics (Allen et al. 2006).

Butterfly richness and composition were also affected by spatial predictors, although their effects tended to be relatively less important. Species richness increased with distance from the Equator and from East to West, and species composition was associated to longitude. Despite these effects, geographic positioning alone was the least important component for explaining butterfly turnover. We found a clear, although weak, decay in compositional similarity with increasing geographical distance, which

indicates that isolation by long geographical distances in Amazonia may limit the dispersal of many organisms. However, the unique contribution of geographical distance to explain butterfly compositional similarity had very little importance. This decay in compositional similarity with geographical distance may represent the effect of environmental differences between sites (Tuomisto et al. 2003). Therefore, our findings are in accordance with the expectation that butterflies have high dispersal capacity, thereby being less likely to be limited by dispersal, even at broad scales.

#### *The role of rivers as barriers to dispersal*

Here we show that butterfly species composition was associated with environment, but areas of endemism limited by large rivers had the largest unique contribution to explain butterfly species turnover. These findings contrast with a recent multi-taxa study, in which environment and areas of endemism had nearly the same unique contribution to explain species distribution, while spatial factors had little relative importance (Dambros et al. 2020). The increased importance of areas of endemism found in our study may be due to our larger sample extent, which included samples from five areas of endemism, rather than only two regions evaluated in the study of Dambros et al. (2020). As more areas of endemism were included in the model, potential effects of river barriers may be more easily detected.

The effectiveness of rivers as barriers to dispersal depend on species traits, as well as the size and type of the river (Ayres and Clutton-Brock 1992, Fouquet et al. 2015). We found that differences in butterfly species composition was more evident between areas of endemism separated by the Amazon and Negro rivers. This is consistent with the evolution of the main west-east Amazonian drainage (Hoorn et al. 2010), which allowed allopatric speciation or accumulation of differences in species composition across the margins of the Amazon River. However, even a large river, such as the Amazon, can work as a ‘suture zone’ (i.e., a region where species have hybrid zones) for butterflies, which indicates a continuous cross-river dispersal (Dasmahapatra et al. 2010, Rosser et al. 2021) and suggests that rivers are more likely to act as partial barriers, rather than absolute barriers to species dispersal.

Despite the apparent effect of river barriers on species composition, areas of endemism are inherently spatially structured, i.e., are correlated with their geographical positioning, thus it may be difficult to separate their independent effects (see discussion

on interactions later on). Although river areas of endemism limited by rivers had the largest unique contribution to explain butterfly turnover, we did not find a clear separation of assemblages among biogeographic regions. When evaluating the effects of geographical distance and differences in areas of endemism on compositional similarity, we did not find evidence of a separation of species composition in opposite river margins, and the largest component explaining compositional similarity was the contribution of environmental distance. Therefore, our findings suggest that the effect of river barriers may result from a combination of factors, especially at broad spatial scales.

#### *Interaction between environment, space and barriers*

Spatial and environmental factors may interact to explain species distribution due to the inherent spatial structure of environmental gradients. In such cases, the correlation between environment and space can hamper teasing apart the effects of one factor or another. For instance, the trend of decreasing compositional similarity between sites with their geographical distance presented reversals at some intervals of geographical distances, which coincided with increases of environmental similarity with increasing geographical distance. Also, butterfly richness tended to increase with distance from the Equator and from East to West (although our sampled longitudinal gradient spanned only ~10 degrees). The highest species richness in the northeastern portion of our sampling extent, coincided with areas where solar radiation reach highest values in our sampled gradient (see Table S1). On the other hand, the richest assemblages in the southwestern region of our sampling extent are located in areas of persistent orographic rainfall due to the Andes (Hooghiemstra and Van Der Hammen 1998). Therefore, the increasing species richness with latitude likely reflects changes in solar radiation, whereas the increased richness with longitude may reflect the climatic stability due to persistent rainfall towards the Andes.

We found that areas of endemism had the largest unique contribution to explain butterfly turnover, but only Guyana region showed a clearly distinct assemblage from other regions. The Guyana region was also clearly different from other regions in terms of environmental conditions (see Fig. S4), so the distinct species composition in this region may be associated to its particular environmental conditions. Although most previous studies have used the categorization of areas of endemism limited by Amazonian rivers as a proxy for dispersal barriers, the effectiveness of such proxy is

unclear and has not been much questioned. This is because areas of endemism can be correlated with both environmental conditions (but see Maximiano et al., 2020) and geographical positioning. Current environmental conditions are likely to be spatially structured among areas of endemism, given the historical climate/drainage dynamics that affected the evolution of Amazonian landscapes (Silva et al. 2019). Also, nearby sites are more likely to be located within the same area of endemism than in different ones, simply due to the natural spatial structure of biogeographical regions. Therefore, in this context, “river barriers” (in this case, areas limited by rivers) are not associated only with barriers to dispersal, but are also correlated with environmental conditions within interfluvial regions. We argue that the use of areas of endemism as a proxy for dispersal barriers in Amazonian biogeographic studies must be seen with caution.

### *Conclusions*

Here we evaluate how environmental and dispersal filters affect the distribution of Amazonian fruit-feeding butterflies, in order to understand the importance of niche and neutral processes at broad scales. Environmental gradients, especially climatic, seem to be strongly associated to butterfly turnover, which suggest that species are specialized to different parts of the environmental gradients (i.e., niche partitioning). The importance of climate in structuring butterfly assemblages are likely related to ectothermic nature of these species, which depend on proper climatic conditions to maintain their normal activity (Turner et al. 1987). The effects of geographic positioning/distance were also clear, although their contribution tended to be less important, suggesting that butterflies are less likely to be limited by dispersal, even at broad scales. Similarly, the effect of river barriers may result from a combination of factors, due to the correlation between environmental conditions and areas of endemism limited by rivers, which are also naturally spatially-structured. Therefore, our findings suggest that environmental conditions are more important than dispersal limitation (isolation by distance or river barriers) to explain the variation in Amazonian butterfly assemblages at broad scales.

## REFERENCES

- Allen, A. P. et al. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. - *Proc. Natl. Acad. Sci. U. S. A.* 103: 9130–9135.
- Ayres, J. M. and Clutton-Brock, T. H. 1992. River boundaries and species range size in Amazonian primates. - *Am. Nat.* 140: 531–537.
- Borges, S. H. and Da Silva, J. M. C. 2012. A new area of endemism for amazonian birds in the rio negro basin. - *Wilson J. Ornithol.* 124: 15–23.
- Boubli, J. P. et al. 2015. Spatial and temporal patterns of diversification on the Amazon: A test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. - *Mol. Phylogenet. Evol.* 82: 400–412.
- Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. - *Ornithol. Monogr.*: 49–84.
- Da Silva, J. M. C. et al. 2002. Differentiation of *Xiphocolaptes* (Dendrocolaptidae) across the river Xingu, Brazilian Amazonia: recognition of a new phylogenetic species and biogeographic implications. - *Bull. Br. Ornithol. Club.* 122: 185–194.
- Da Silva, J. M. C. et al. 2005. The fate of the Amazonian areas of endemism. - *Conserv. Biol.* 19: 689–694.
- Dambros, C. S. et al. 2017. Isolation by distance, not rivers, control the distribution of termite species in the Amazonian rain forest. - *Ecography* 40: 1242–1250.
- Dambros, C. et al. 2020. The role of environmental filtering, geographic distance and dispersal barriers in shaping the turnover of plant and animal species in Amazonia. - *Biodivers. Conserv.* 29: 3609–3634.
- Dasmahapatra, K. K. et al. 2010. The anatomy of a “suture zone” in Amazonian butterflies: A coalescent-based test for vicariant geographic divergence and speciation. - *Mol. Ecol.* 19: 4283–4301.
- De Bie, T. et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. - *Ecol. Lett.* 15: 740–747.

- Dias-Terceiro, R. G. et al. 2015. A Matter of Scale: Historical and Environmental Factors Structure Anuran Assemblages from the Upper Madeira River, Amazonia. - *Biotropica* 47: 259–266.
- Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. - *Int. J. Climatol.* 37: 4302–4315.
- Fluck, I. E. et al. 2020. Climate and geographic distance are more influential than rivers on the beta diversity of passerine birds in Amazonia. - *Ecography* 43: 860–868.
- Fouquet, A. et al. 2015. The trans-riverine genetic structure of 28 Amazonian frog species is dependent on life history. - *J. Trop. Ecol.* 31: 361–373.
- Freitas, A. V. . et al. 2006. Insetos como Indicadores de Conservação da Paisagem. - In: *Biologia da Conservação e Manejo da Vida Silvestre*. pp. 357–384.
- Freitas, A. V. L. et al. 2014. Studies with butterfly bait traps: an overview. - *Rev. Colomb. Entomol.* 40: 203–212.
- Goslee, S. C. and Urban, D. L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. - *J. Stat. Softw.* 22: 1–19.
- Guilherme D. R. et al. 2021. Direct and indirect effects of geographic and environmental factors on ant beta diversity across Amazon basin. - *Oecologia*. In press. <https://doi.org/10.1007/s00442-021-05083-7>
- Graça, M. B. et al. 2015. Combining Taxonomic and Functional Approaches to Unravel the Spatial Distribution of an Amazonian Butterfly Community. - *Environ. Entomology* 45: 301–309.
- Hawkins, B. A. and Porter, E. E. 2003. Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies. - *Ecol. Entomol.* 28: 678–686.
- Hawkins, B. et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. - *Ecology* 84: 3105–3117.
- Hooghiemstra, H. and Van Der Hammen, T. 1998. Neogene and Quaternary development of the neotropical rain forest: The forest refugia hypothesis, and a literature overview. - *Earth Sci. Rev.* 44: 147–183.

- Hoorn, C. et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. - *Science* (80-. ). 330: 927–931.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. - Princeton University Press.
- Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. - *Funct. Ecol.* 19: 166–172.
- Legg, G. 1978. A note on the diversity of World Lepidoptera (Rhopalocera). - *Biol. J. Linn. Soc.* 10: 343–347.
- Leibold, M. A. and Mikkelsen, G. M. 2002. Coherence , species turnover, and boundary clumping : elements of meta-community structure. - *Oikos* 97: 237–250.
- Magnusson, W. E. et al. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. - *Biota Neotrop.* 5: 21–26.
- Maximiano, M. F. de A. et al. 2020. The relative role of rivers, environmental heterogeneity and species traits in driving compositional changes in southeastern Amazonian bird assemblages. - *Biotropica* 52: 946–962.
- Menéndez, R. et al. 2007. Direct and indirect effects of climate and habitat factors on butterfly diversity. - *Ecology* 88: 605–611.
- Naka, L. N. 2011. Avian distribution patterns in the Guiana Shield: implications for the delimitation of Amazonian areas of endemism. - *J. Biogeogr.* 38: 681–696.
- Oksanen, A. J. et al. 2013. *vegan: Community Ecology Package*.
- Penz, C. et al. 2015. Butterfly dispersal across Amazonia and its implication for biogeography. - *Ecography (Cop.)*. 38: 410–418.
- R Development Core Team 2018. *R: A language and environment for statistical computing*. - R Foundation for Statistical Computing.
- Rabelo, R. M. et al. 2021. The Role of River Flooding as an Environmental Filter for Amazonian Butterfly Assemblages. - *Front. Ecol. Evol.* 9: 693178.
- Ribas, C. C. et al. 2012. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. - *Proc. Biol. Sci.* 279: 681–9.

- Ribeiro, D. B. and Freitas, A. V. L. 2012. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. - *J. Insect Conserv.* 16: 733–744.
- Rosser, N. et al. 2021. The Amazon river is a suture zone for a polyphyletic group of co-mimetic heliconiine butterflies. - *Ecography (Cop.)*. 44: 177–187.
- Santorelli, S. et al. 2018. Most species are not limited by an Amazonian river postulated to be a border between endemism areas. - *Sci. Rep.* 8: 1–8.
- Sawada, Y. et al. 2015. A new 500-m resolution map of canopy height for Amazon forest using spaceborne LiDAR and cloud-free MODIS imagery. - *Int. J. Appl. Earth Obs. Geoinf.* 43: 92–101.
- Silva, S. M. et al. 2019. A dynamic continental moisture gradient drove Amazonian bird diversification. - *Sci. Adv.* 5: eaat5752 3.
- Stefanescu, C. et al. 2011. Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. - *Ecography (Cop.)*. 34: 353–363.
- Svenning, J. C. et al. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. - *J. Anim. Ecol.* 80: 393–402.
- Tuomisto, H. et al. 2003. Dispersal, environment, and floristic variation of Western Amazonian forests. - *Science (80-. )*. 299: 241–244.
- Tuomisto, H. et al. 2016. A compositional turnover zone of biogeographical magnitude within lowland Amazonia. - *J. Biogeogr.* 43: 2400–2411.
- Turner, J. R. G. et al. 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. - *Oikos* 48: 195–205.
- Warren, D. L. et al. 2014. Mistaking geography for biology: inferring processes from species distributions. - *Trends Ecol. Evol.* 29: 572–580.
- White, P. and Kerr, J. T. 2006. Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. - *Ecography (Cop.)*. 29: 908–918.

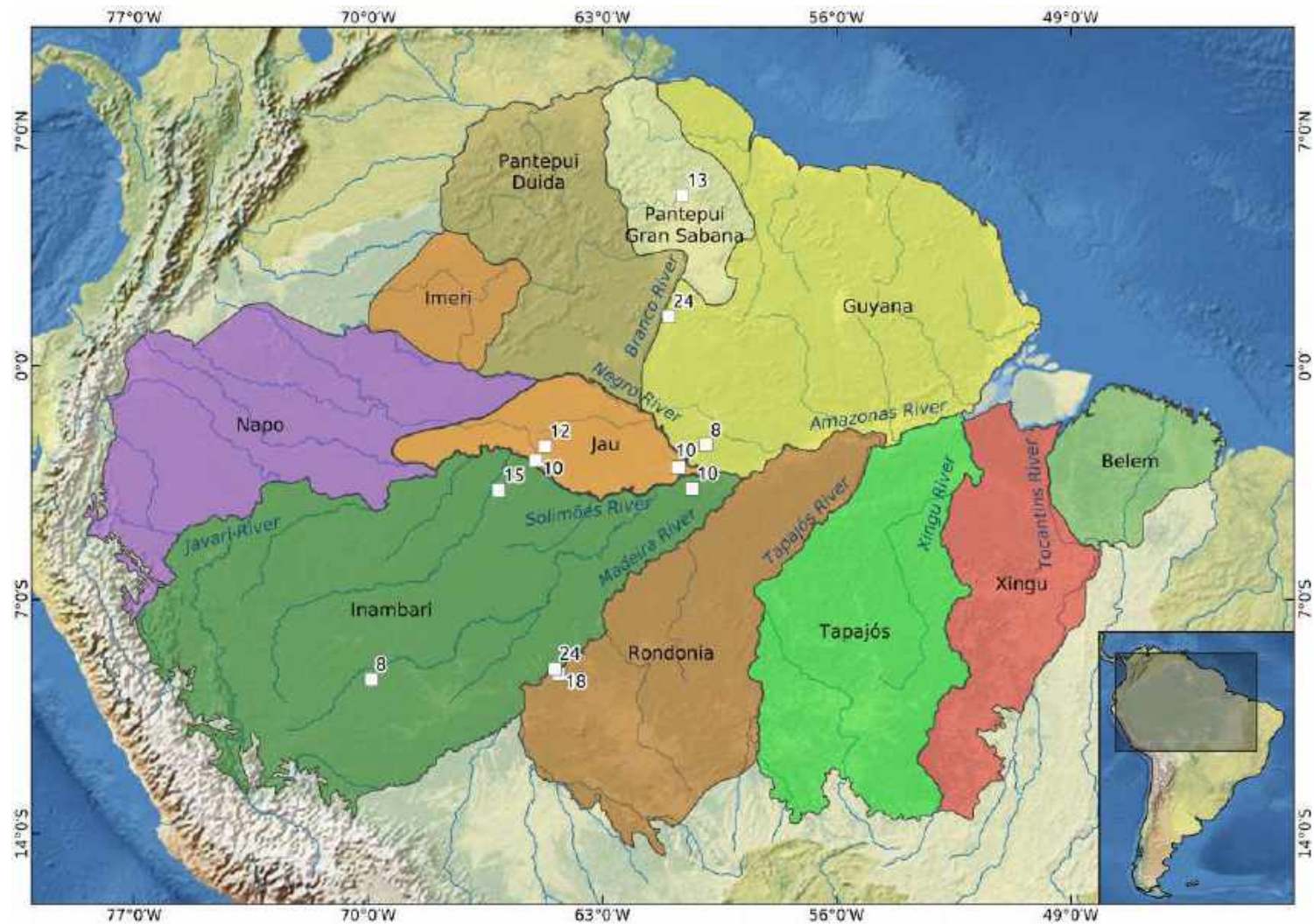
Zuquim, G. et al. 2012. Broad Scale Distribution of Ferns and Lycophytes along Environmental Gradients in Central and Northern Amazonia, Brazil. - *Biotropica* 44: 752–762.

Zuquim, G. et al. 2019. Making the most of scarce data: Mapping soil gradients in data-poor areas using species occurrence records. - *Methods Ecol. Evol.* 10: 788–801.

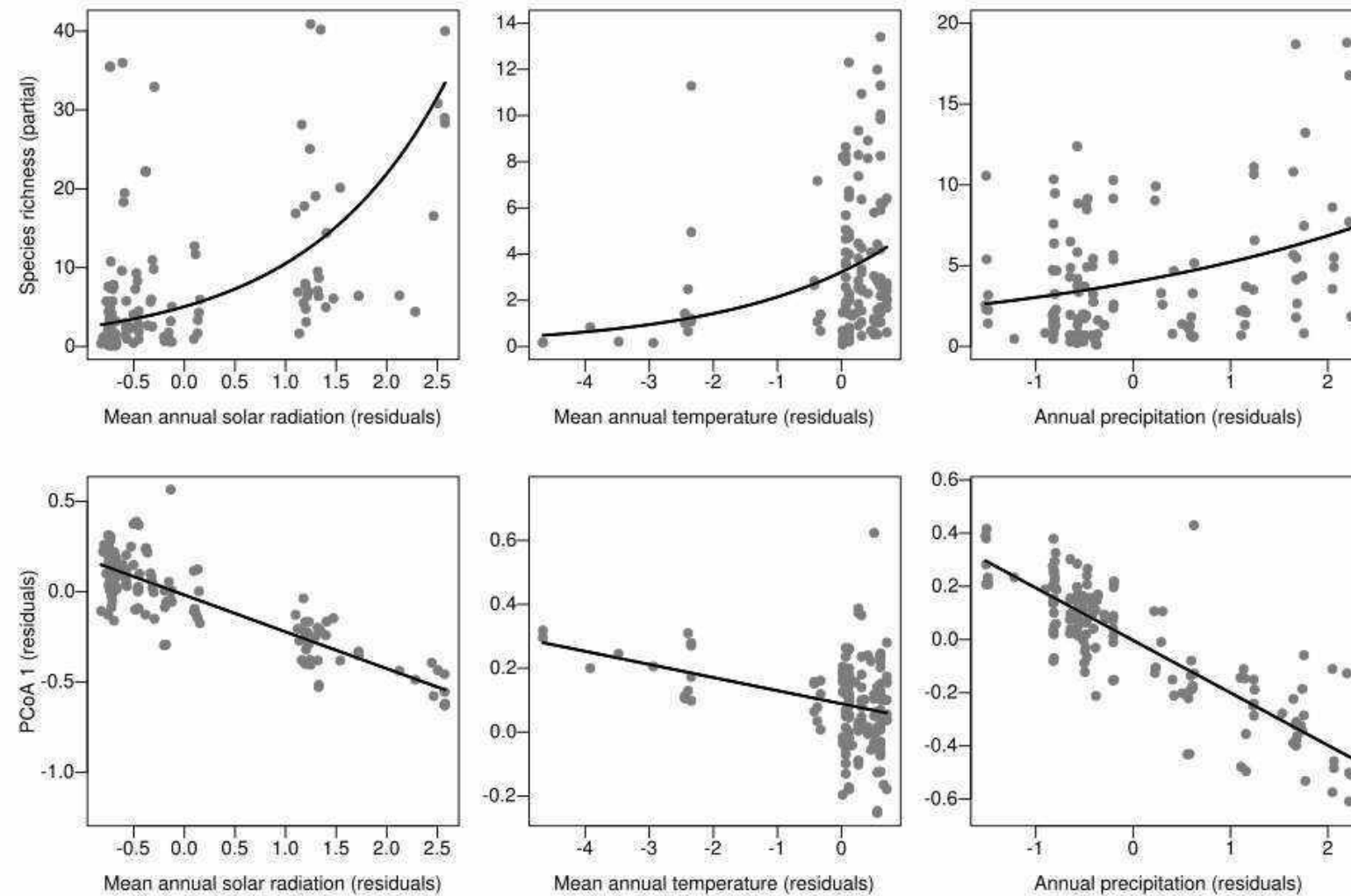
**Table 1.** Coefficients from multiple regression models for the effects of geographic position, areas of endemism and environmental variables on species richness and composition. Model for species richness was performed considering a Poisson distribution. Species composition represents the species turnover, which was summarized by the first axis of an PCoA ordination based on a Jaccard index. Model selection was based on AICc (Table S3 and S4) and only variables included in the best model are shown. Bold coefficients represent significant values at  $p < 0.05$ . (—) indicates variables not included in the model; NA are variables not included in the analysis.

|                                 | Species Richness | Species Composition (PCoA 1) |
|---------------------------------|------------------|------------------------------|
| Guyana/Intercept                | NA               | <b>6.79</b>                  |
| Gran Sabana                     | NA               | <b>-2.34</b>                 |
| Jau                             | NA               | <b>-6.41</b>                 |
| Inambari                        | NA               | <b>-6.01</b>                 |
| Rondonia                        | NA               | <b>-5.59</b>                 |
| Tree cover (%)                  | <b>-2.94</b>     | -1.57                        |
| Canopy height                   | —                | —                            |
| Clay content                    | —                | —                            |
| Sand content                    | —                | <b>-3.98</b>                 |
| Soil cation concentration       | -1.64            | <b>-3.12</b>                 |
| Mean annual temperature         | <b>4.50</b>      | -0.80                        |
| Annual precipitation            | <b>2.16</b>      | <b>-3.45</b>                 |
| Mean annual solar radiation*    | <b>4.88</b>      | <b>-2.08</b>                 |
| Latitude                        | -0.21            | 0.13                         |
| Longitude                       | <b>-5.49</b>     | <b>-4.70</b>                 |
| R <sup>2</sup> environment only | 0.13             | 0.13                         |
| R <sup>2</sup> space only       | 0.10             | 0.07                         |
| R <sup>2</sup> endemism only    | NA               | 0.18                         |
| R <sup>2</sup> total            | 0.24             | 0.44                         |

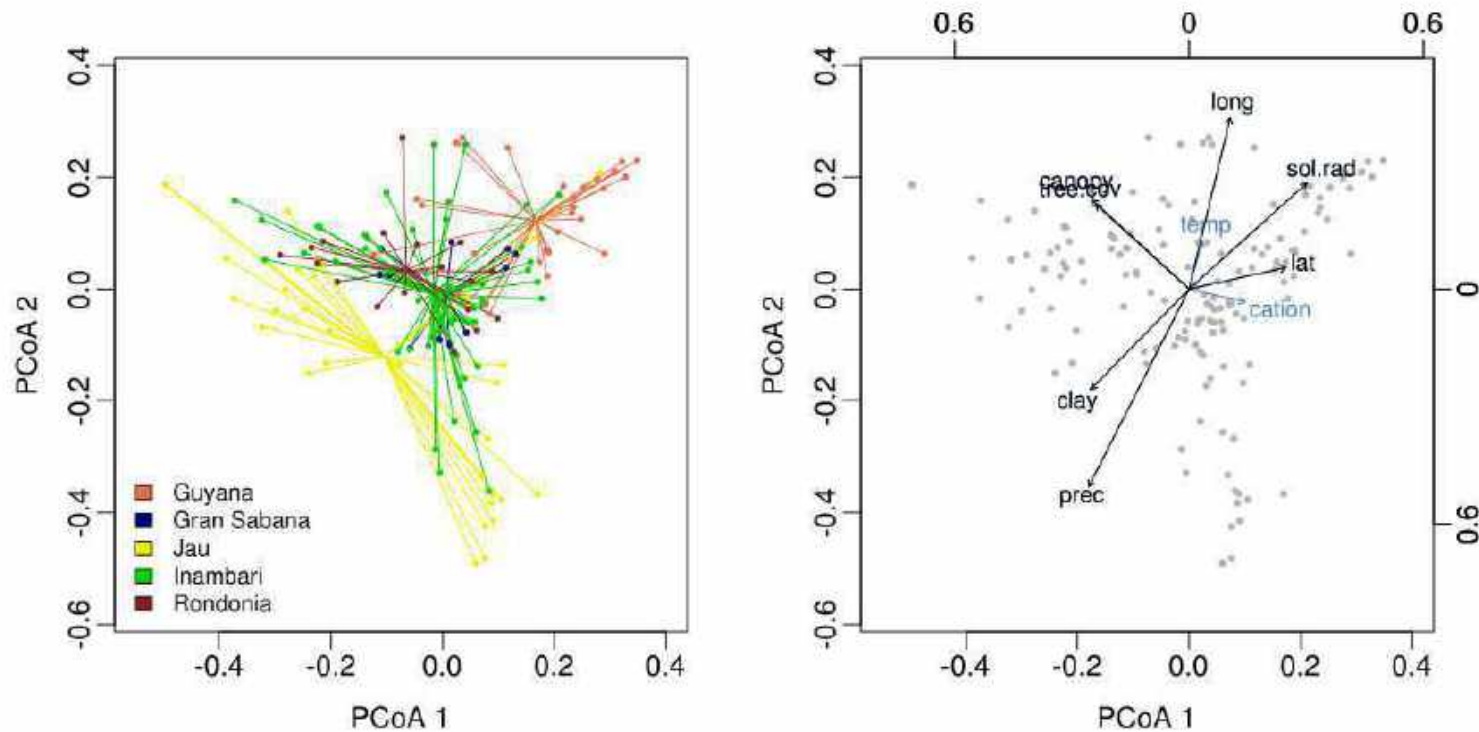
\*Solar radiation was highly correlated with latitude, so its effects were estimated separately along with other predictors, except for latitude, which was substituted by the module of latitude (i.e., distance from Equator).



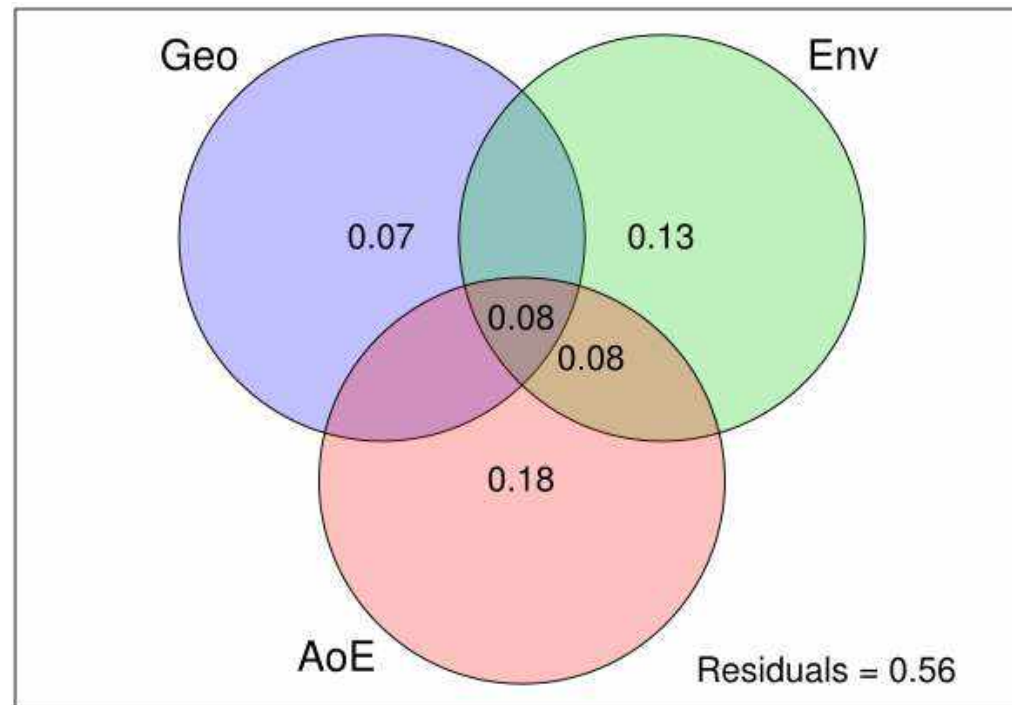
**Figure 1.** Distribution of sampling plots across Amazonia. White squares show the location of sampling grids and adjacent numbers indicate the number of sampling plots surveyed in each grid.



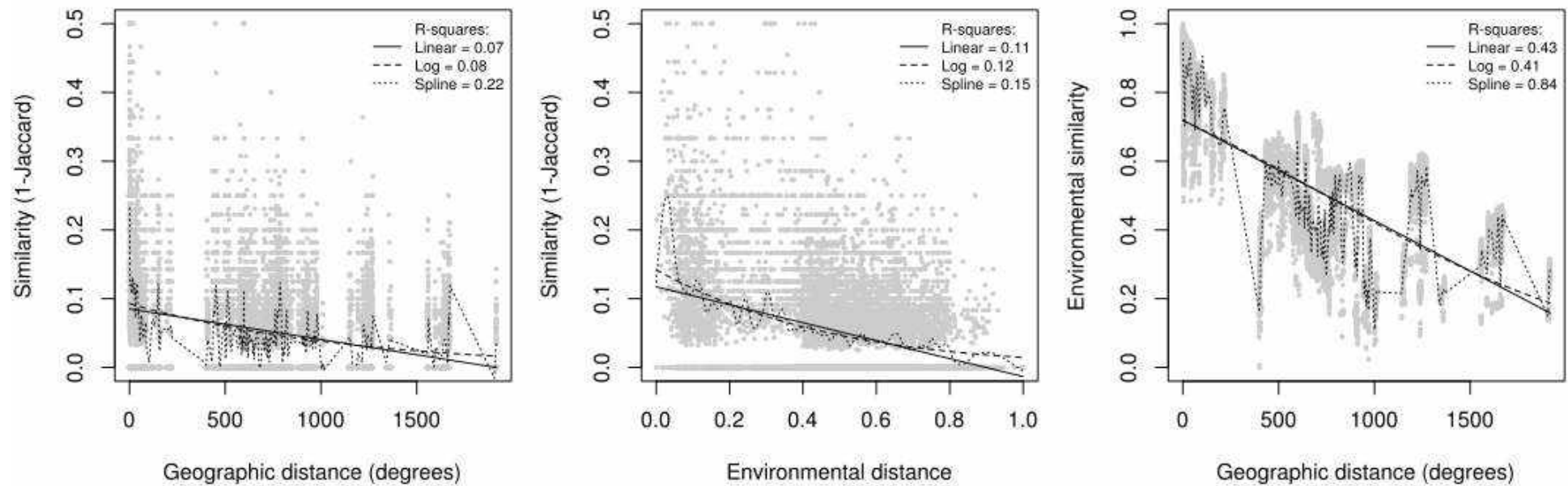
**Figure 2.** Independent responses of species richness and composition (y-axes) to climatic variables (x-axis). Graphs represent the partial responses according to multiple regression models.



**Figure 3.** Ordination plots according to a Principal Coordinate Analysis (PCoA) to summarize similarities in Amazonian butterfly assemblages. Distance between points represent their similarity between plots according to their species composition. Colors in the left graph represent the major bird areas of endemism, and distance among group centroids may be interpreted as differences in species composition among groups. Arrows length in the right graph show the correlation of variables with PCoA 1 or 2. Black and blue arrows indicate significant and non-significant correlations of variables and PCoA axes, respectively. lat = latitude; long = longitude; sol.rad = mean annual solar radiation; temp = mean annual temperature; prec = annual precipitation; cation = soil cation concentration; clay = soil clay content; trecov = % of tree cover; canopy = canopy height.



**Figure 4.** Venn diagram showing the relative contribution ( $R^2$ ) of geographical position (Geo); environmental variables (Env) and areas of endemism (AoE) to explain butterfly compositional turnover in Amazonia. Compositional turnover was measured by a Principal Coordinate Analysis (PCoA), based on the Jaccard index. Relative contributions were determined using multiple regressions and variance partitioning. Values show the amount of variance that was uniquely or jointly explained by the components. Components with  $R^2 < 0$  are not shown.



**Figure 5.** Decay of compositional dissimilarity with geographical distance and environmental difference among 148 sample plots. Each gray point represents a pair of sites being compared. Butterfly similarity (Jaccard index) between sites are plotted against their geographical and environmental distances in left and middle graphs. Environmental similarity between sites is plotted against their geographic distance in the right graph. Environmental similarity is the complement of the environmental distance. Linear, logarithm and flexible splines curves are shown to represent changes in the average similarity with increasing distance. Flexible spline function gives the most accurate representation of changes in average similarity.

## Síntese

Nessa tese, eu investiguei como processos de dispersão e ambientais podem afetar a distribuição de borboletas Amazônicas em diferentes escalas espaciais, por meio de filtros de dispersão, ambientais e bióticos. No Capítulo I, eu avaliei o papel dos processos históricos, sob uma perspectiva biogeográfica, estudando as mudanças no padrão de distribuição das espécies ao longo do tempo geológico. Demonstrei como a distribuição de *Antirrhea ulei*, uma espécie rara e altamente adaptada a condições ambientais específicas, é influenciada fortemente por gradientes ambientais. Essa forte associação da espécie com seus requerimentos ambientais foi utilizada para construir um modelo que foi utilizado para prever a distribuição espacial histórica da espécie até o presente. Essas projeções permitiram testar a hipótese de que a espécie provavelmente possuiu uma extensão mais ampla de habitats adequados durante o último máximo glacial e pode ter ocupado grande parte do Pantepui oriental, migrando para alto dos tepuis atuais assim que seu habitat adequado foi sendo perdido durante o aquecimento do Holoceno. Esses resultados estão de acordo com a Hipótese de Migração por Vicariância (Rull, 2005) e ajudam a entender a evolução da biodiversidade do Pantepui.

No Capítulo II, investiguei como os filtros ambientais e bióticos podem atuar para determinar a abundância, o número e a composição de espécies de borboletas em escalas locais em um gradiente de inundação e suas mudanças ambientais associadas. Encontrei que as florestas de várzea possuem maior abundância e densidade de espécies, provavelmente devido à alta produtividade primária dessas florestas. Também encontrei uma diferença pronunciada na composição de espécies entre várzea e terra firme, com espécies sendo substituídas de um tipo florestal ao outro, devido às mudanças ambientais e bióticas entre esses tipos florestais. Discuti como as condições ambientais podem selecionar a evolução de traços e comportamentos adaptativos, os quais podem afetar a habilidade das espécies de dispersar e persistir em sítios locais. Os achados desse estudo reforçam que a inundação em florestas alagáveis da Amazônia é um importante filtro ambiental, o qual determina fortemente a distribuição de espécies de borboletas, bem como a distribuição das espécies com as quais elas interagem, tais como suas plantas hospedeiras.

Por fim, no Capítulo III, avaliei como os filtros ambientais e de dispersão afetam a distribuição de borboletas frugívoras Amazônicas, com o intuito de entender a importância de processos neutro e de nicho em amplas escalas. Encontrei que as espécies são gradualmente substituídas ao longo de gradientes ambientais, especialmente climáticos, sugerindo que as espécies são especializadas em diferentes partes dos gradientes ambientais, particionando seus nichos para

permitir a coexistência (Hubbell, 2001). A importância do clima na estruturação das assembleias de borboletas provavelmente está relacionada a natureza ectotérmica dessas espécies, que dependem de condições climáticas apropriadas para manterem suas atividades normais (Turner, Gatehouse e Corey, 1987). Também observei um efeito da distância e posição geográfica dos sítios, embora esses efeitos tenderam a ser menos importantes, sugerindo que as borboletas são menos prováveis de serem limitadas por filtros de dispersão, mesmo em amplas escalas. Encontrei que os efeitos parciais dos grandes rios amazônicos como barreiras geográficas à dispersão das espécies, pode ser o resultado de uma combinação de fatores, devido à correlação entre as condições ambientais e áreas interfluviais de endemismo delimitada por rios, as quais também são espacialmente estruturadas. Portanto, esses resultados sugerem que as limitações ambientais são mais importantes que a limitação por dispersão (por isolamento ou barreiras geográficas) para explicar a distribuição de borboletas Amazônicas em amplas escalas.

## Referências bibliográficas

- BARLOW, J. *et al.* Diversity and composition of fruit-feeding butterflies in tropical *Eucalyptus* plantations. **Biodiversity and Conservation**, v. 17, n. 5, p. 1089–1104, 2008.
- BOUBLI, J. P. *et al.* Spatial and temporal patterns of diversification on the Amazon: A test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. **Molecular Phylogenetics and Evolution**, v. 82, n. PB, p. 400–412, 2015.
- BROWN JR, K. S. Geologic, evolutionary, and ecological bases of the diversification of neotropical butterflies: Implications for conservation. *In*: BERMINGHAM, E.; DICKAND, C.; MORITZ, C. (Eds.). . **Tropical rainforests: Past, present, and future**. Chicago: The University of Chigado Press, 2005. p. 166–201.
- BROWN JR, K. S.; FREITAS, A. V. L. Atlantic Forest Butterflies: Indicators for Landscape Conservation. **Biotropica**, v. 32, n. 4b, p. 934–956, 2000.
- DAMBROS, C. *et al.* The role of environmental filtering, geographic distance and dispersal barriers in shaping the turnover of plant and animal species in Amazonia. **Biodiversity and Conservation**, v. 29, n. 13, p. 3609–3634, 2020.
- DAMBROS, C. S. *et al.* Isolation by distance, not rivers, control the distribution of termite species in the Amazonian rain forest. **Ecography**, v. 40, p. 1242–1250, 2017.
- DIAS-TERCEIRO, R. G. *et al.* A Matter of Scale: Historical and Environmental Factors Structure Anuran Assemblages from the Upper Madeira River, Amazonia. **Biotropica**, v. 47, n. 2, p. 259–266, 2015.
- FREITAS, A. V. . *et al.* Insetos como Indicadores de Conservação da Paisagem. *In*: **Biologia da Conservação e Manejo da Vida Silvestre**. [s.l: s.n.]. p. 357–384.
- GARDNER, T. A. *et al.* The cost-effectiveness of biodiversity surveys in tropical forests. **Ecology Letters**, v. 11, p. 139–150, 2008.
- GRAÇA, M. B. *et al.* Combining Taxonomic and Functional Approaches to Unravel the Spatial Distribution of an Amazonian Butterfly Community. **Environmental Entomology**, v. 45, p. 301–309, 2015.
- \_\_\_\_. Taxonomic, functional, and phylogenetic perspectives on butterfly spatial assembly in northern Amazonia. **Ecological Entomology**, v. 42, p. 816–826, 2017.

- GUILHERME, D. R. *et al.* Direct and indirect effects of geographic and environmental factors on ant beta diversity across Amazon basin. **Oecologia**, v. Early View, 2021.
- HUBBELL, S. P. **The unified neutral theory of biodiversity and biogeography**. Princenton: Princenton University Press, 2001.
- IRION, G. *et al.* Development of the Amazon valley during the middle to late Quaternary: sedimentological and climatological observations. In: JUNK J. W. *et al.* (Eds.). **Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management**. New York: Springer, 2010. p. 27–42.
- LEGG, G. A note on the diversity of World Lepidoptera (Rhopalocera). **Biological Journal of the Linnean Society**, v. 10, n. 3, p. 343–347, 1978.
- LEIBOLD, M. A. *et al.* The metacommunity concept: a framework for multi-scale community ecology. **Ecology Letters**, v. 7, n. 7, p. 601–613, 4 jun. 2004.
- MENÉNDEZ, R. *et al.* Direct and indirect effects of climate and habitat factors on butterfly diversity. **Ecology**, v. 88, n. 3, p. 605–611, 2007.
- PENZ, C. *et al.* Butterfly dispersal across Amazonia and its implication for biogeography. **Ecography**, v. 38, n. 4, p. 410–418, 2015.
- RIBAS, C. C. *et al.* A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. **Proceedings of the Royal Society B: Biological Sciences**, v. 279, n. 1729, p. 681–689, 2012.
- RIBEIRO, D. B.; FREITAS, A. V. L. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. **Journal of Insect Conservation**, v. 16, p. 733–744, 2012.
- RULL, V. Biotic diversification in the Guayana Highlands: A proposal. **Journal of Biogeography**, v. 32, n. 6, p. 921–927, 2005.
- RULL, V.; VEGAS-VILARRÚBIA, T. Pantepui as a dynamic biogeographical concept. In: RULL, V. *et al.* (Eds.). **Biodiversity of Pantepui: the pristine “Lost World” of the Neotropical Guiana Highlands**. London: Elsevier, 2019. p. 55–67.
- SANTOS, J. P. *et al.* Effects of landscape modification on species richness patterns of fruit-feeding butterflies in Brazilian Atlantic Forest. **Diversity and Distributions**, v. 26, p. 196–208, 2020.

- STEFANESCU, C.; CARNICER, J.; PEÑUELAS, J. Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. **Ecography**, v. 34, p. 353–363, 2011.
- TUOMISTO, H.; RUOKOLAINEN, K.; YLI-HALLA, M. Dispersal, environment, and floristic variation of Western Amazonian forests. **Science**, v. 299, n. 5604, p. 241–244, 2003.
- TURNER, J. R. G.; GATEHOUSE, C. M.; COREY, C. A. Does solar energy control organic diversity? Butterflies, moths and the British climate. **Oikos**, v. 48, n. 2, p. 195–205, 1987.
- WARREN, D. L. *et al.* Mistaking geography for biology: inferring processes from species distributions. **Trends in Ecology and Evolution**, v. 29, n. 10, p. 572–580, 2014.

**APÊNDICE A - MATERIAL SUPLEMENTAR DO ARTIGO PUBLICADO EM**  
*Insect Conservation and Diversity* (Capítulo I)

**SUPPORTING INFORMATION**

**Finding a lost species in the “Lost World”: predicted habitat occupancy by an endemic butterfly in a Neotropical sky-island archipelago**

R.M. Rabelo, I.F. Oliveira and W.E. Magnusson

**Table S1.** Detection history of *Antirrhea ulei* across sample sites at Uei tepui. A1 to A4 show the number of independent detections of the species at each sampling occasion, i.e., at each pair of baiting traps, of each sample site. Effort shows the number of surveyed days (sampling effort) on each sample site.

| Plot  | Latitude | Longitude | A1 | A2 | A3 | A4 | Effort |
|-------|----------|-----------|----|----|----|----|--------|
| SS1P1 | 5,12083  | -60,59747 | 0  | 0  | 0  | 0  | 12     |
| SS1P2 | 5,11697  | -60,59486 | 0  | 0  | 0  | 0  | 12     |
| SS1P3 | 5,11278  | -60,59319 | 0  | 0  | 0  | 0  | 12     |
| SS1P4 | 5,10850  | -60,59500 | 0  | 0  | 0  | 0  | 12     |
| SS2P1 | 5,12319  | -60,59883 | 0  | 0  | 0  | 0  | 8      |
| SS2P2 | 5,11958  | -60,60322 | 0  | 0  | 0  | 0  | 8      |
| SS2P3 | 5,11544  | -60,60767 | 0  | 0  | 0  | 0  | 8      |
| SS2P4 | 5,11128  | -60,61178 | 0  | 0  | 0  | 0  | 8      |
| SS3P1 | 5,09264  | -60,60328 | 0  | 0  | 0  | 0  | 8      |
| SS3P2 | 5,08728  | -60,60575 | 1  | 0  | 0  | 0  | 8      |
| SS3P3 | 5,05514  | -60,60925 | 1  | 0  | 0  | 1  | 8      |
| SS3P4 | 5,04956  | -60,60858 | 1  | 1  | 2  | 4  | 8      |
| SS4P1 | 5,04933  | -60,61272 | 0  | 0  | 0  | 0  | 6      |
| SS4P2 | 5,04683  | -60,6135  | 0  | 0  | 0  | 1  | 6      |

**Table S2.** Variables used in the model. PC1, PC2 and PC3 columns show the correlation of each variable with the axes of a PCA ordination. The amount of variation explained by PC1, PC2 and PC3 was 56%, 23% and 14%, respectively.

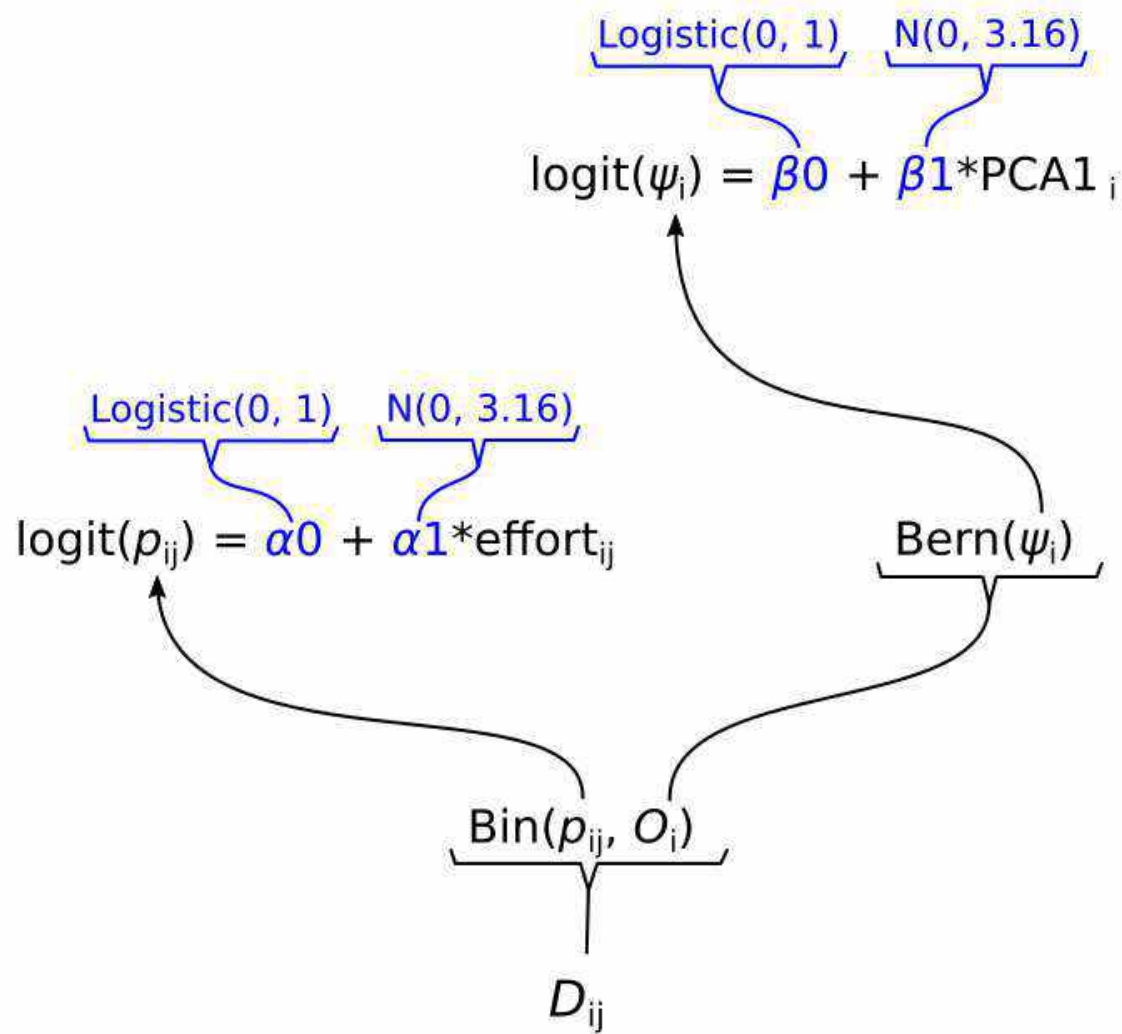
| Type       | Variable  | PC1   | PC2   | PC3   |
|------------|---|-------|-------|-------|
| Climatic   | Bio1 – Annual Mean Temperature <sup>1</sup>       | -0,74 | -0,68 | 0,1   |
|            | Bio4 – Temperature Seasonality <sup>1</sup>       | -0,7  | -0,63 | 0,02  |
|            | Bio7 – Temperature Annual Range <sup>1</sup>      | -0,13 | 0,43  | -0,27 |
|            | Bio12 – Annual Precipitation <sup>1</sup>         | 0,54  | 0,44  | -0,24 |
|            | Bio15 – Precipitation Seasonality <sup>1</sup>    | -0,65 | 0,59  | -0,19 |
| Vegetation | % Tree cover <sup>2</sup>                         | 0,72  | -0,17 | -0,4  |
|            | Canopy height <sup>3</sup>                        | 0,67  | -0,48 | -0,78 |
| Topography | Elevation <sup>4</sup>                            | 0,68  | 0,16  | -0,62 |
|            | HAND (height above nearest drainage) <sup>4</sup> | 0,5   | -0,52 | -0,13 |

<sup>1</sup>Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315.

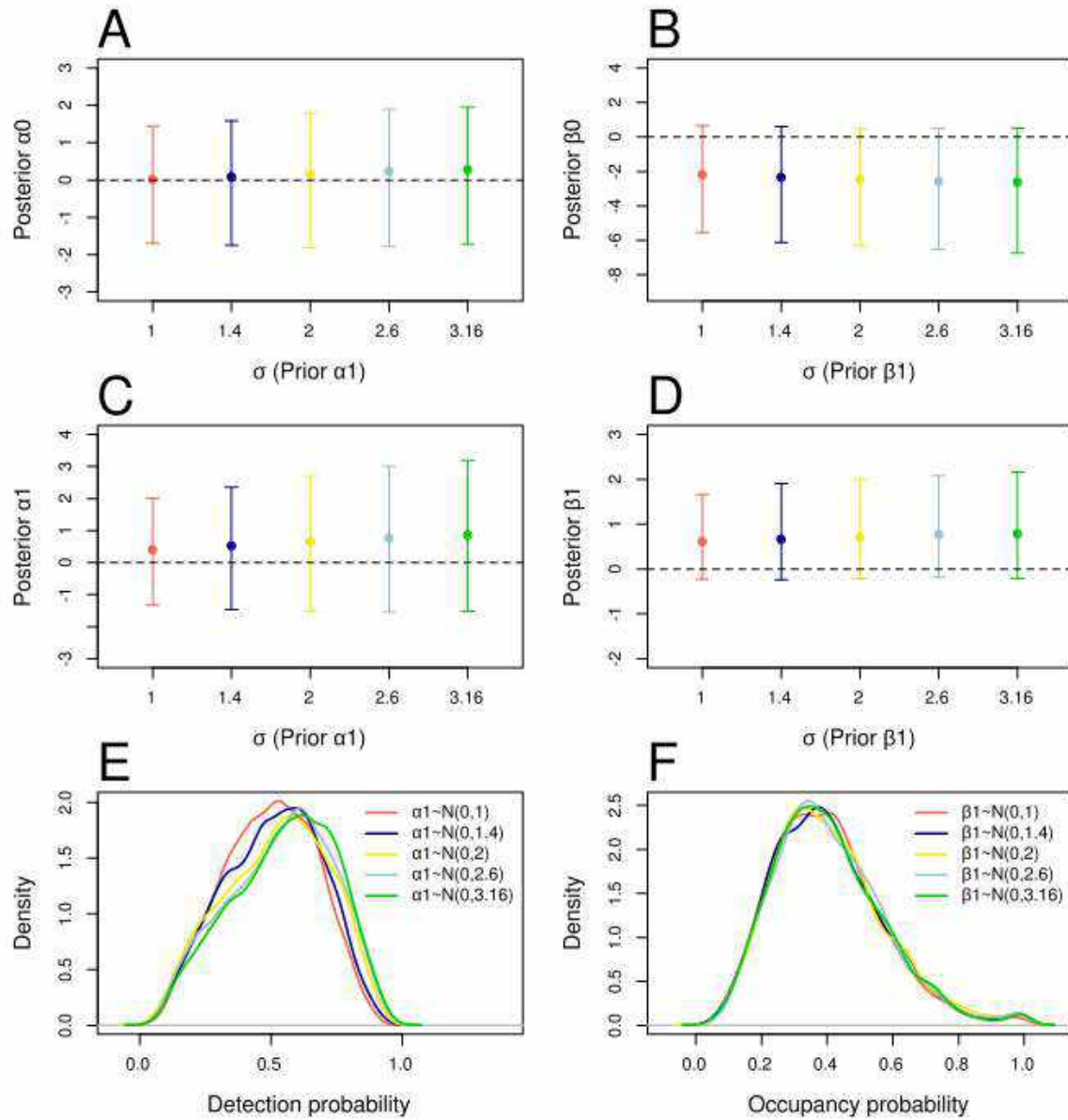
<sup>2</sup>Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. & Townshend, J.R.G. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**(6160), 850–853.

<sup>3</sup>Sawada, Y., Suwa, R., Jindo, K., Endo, T., Oki, K., Sawada, H., Arai, E., Shimabukuro, Y.E., Celes, C.H.S., Campos, M.A.A. & Higuchi, F.G. (2015) A new 500-m resolution map of canopy height for Amazon forest using spaceborne LiDAR and cloud-free MODIS imagery. *International Journal of Applied Earth Observation and Geoinformation*, **43**, 92-101.

<sup>4</sup>DPI-INPE – Divisão de Processamento de Imagens – Instituto Nacional de Pesquisas Espaciais (2018) *Ambidata – Variáveis ambientais para modelagem de distribuição de espécies* <<http://www.dpi.inpe.br/Ambidata/>> 15th August 2018.



**Figure S1.** Representation of the Bayesian hierarchical occupancy model formulation used in the study. Blue coefficients represent the estimated model parameters, for which we provided vague priors. We specified logistic priors for intercepts, which imply in Uniform(0,1) priors for detection and occupancy probabilities in the probability scale, and normal priors with  $\mu = 0$  and  $\sigma = 3.16$  for coefficients describing the effects of covariates detection and occupancy probabilities in the logit scale.



**Figure S2.** Prior sensitivity analysis on posterior estimates. Effects of sequentially smaller values of  $\sigma$  of priors for  $\alpha_1$  and  $\beta_1$  (1, 1.4, 2, 2.6 and 3.16) on posterior estimates of model parameters (A–D) and on detection and occupancy probabilities (E and F). In A–D, points represent the median and lines represent Bayesian credible intervals of posterior estimates for model coefficients. In E and F, lines show the posterior distribution of detection (E) and occupancy (F) probabilities.

## Appendix S1. R code for model implementation.

```
#####
## Modelling A. ulei distribution in the Pantepui
##
## script by Rafael Rabelo -- last edited Jun 2021
#####

library(rjags)

##~~~~~
## Model formulation
##~~~~~

## writing model diagram
model<- "
  model{
    ## Occupancy and detection modelling
    for(i in 1:nsites){
      for(j in 1:noccasions){
        aulei[i,j]~dbinom(det[i] * occ[i], 1)
      }

      ## Detection as a function of effort
      detLinear[i]<- e0 + e1*EFFORT[i]
      det[i]<- exp(detLinear[i])/(1 + exp(detLinear[i]))

      ## Occupancy as a function of PCA axes
      psiLinear[i]<- b0 + b1*PCA1[i]
      psi[i]<- exp(psiLinear[i])/(1 + exp(psiLinear[i]))
      occ[i]~dbinom(psi[i], 1)
    }

    ## Priors
    e0~dlogis(0,1)
    e1~dnorm(0,1/3.16)
    b0~dlogis(0,1)
    b1~dnorm(0,1/3.16)
  }
"

## Exporting model
writeLines(model, con="modelAulei.jags")

##~~~~~
## Model implementation
##~~~~~

## Creating the data. Here I need to provide the
## names of each data as they appear within the
## model code, i.e., the diagram.
Aulei.data<- list(aulei=aulei, ## detection data
                  nsites=nrow(aulei), ## number of sites
                  noccasions=ncol(aulei), ## number of occasions
                  EFFORT=effort[1:14,], ## sampling effort (scaled)
                  PCA1=PCA1) ## environmental variables (PCA1)

## Burn-in
ppModel<- jags.model("modelAulei.jags",
                    data = Aulei.data,
```

```

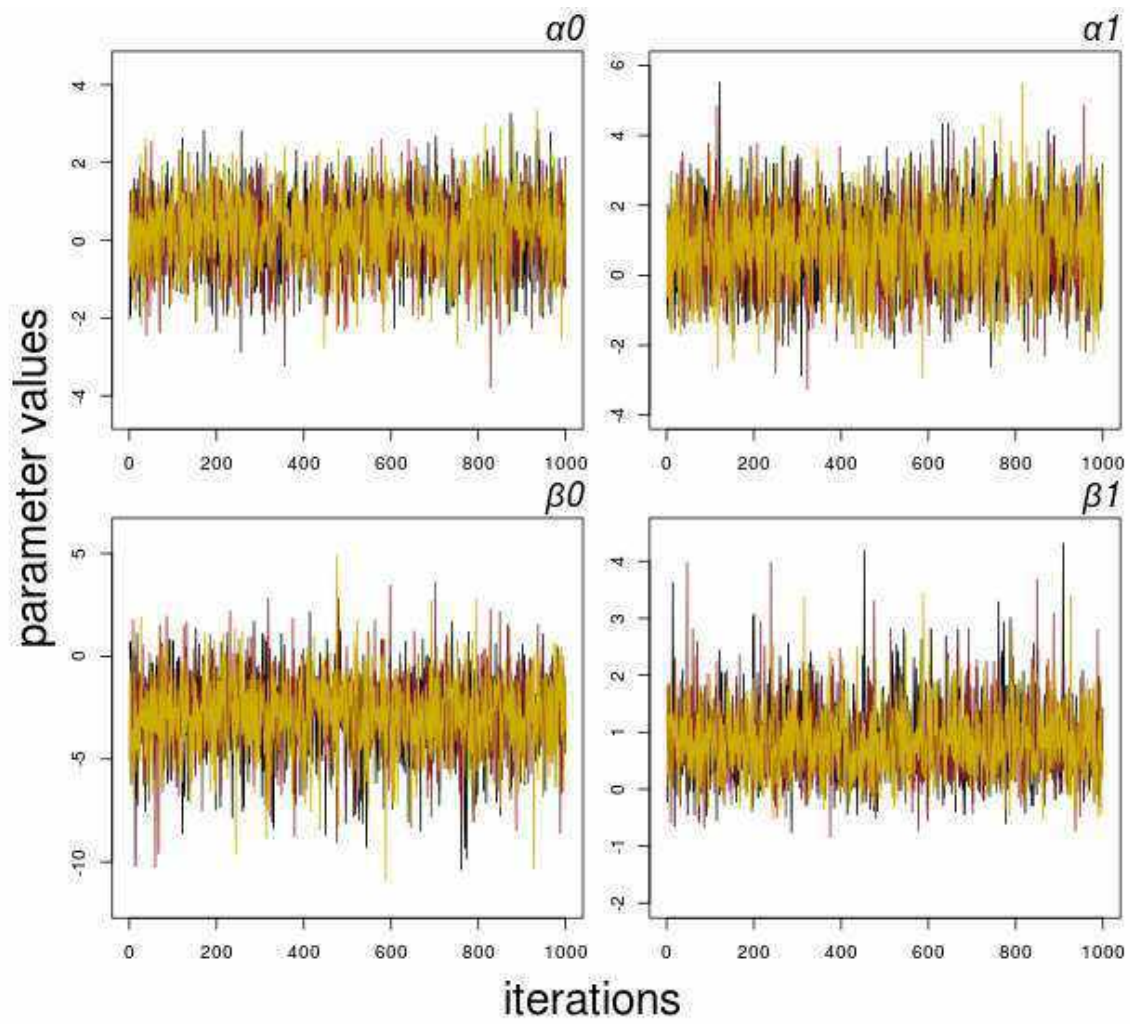
        n.chains = 3,
        n.adapt = 10000,
        inits = list(occ = rep(1,14)))

## Parameters estimates after chains convergence
ppResu<- coda.samples(ppModel,
                      variable.names = c("e0", "e1", "b0", "b1"),
                      n.iter = 100000,
                      thin = 100)

## transforming the results into a matrix
resu.mat<- as.matrix(ppResu); head(resu.mat)

## THE END!
#####

```



**Figure S3.** Chains convergence. Trace plots showing the variation of parameter estimates along the iterations of Markov chains, after removal of burn-in steps. Golden, brown and black lines represent each of the three parallel chains. It is possible to observe the chain convergence in parameter estimates along iterations for all model parameters.

**APÊNDICE B - MATERIAL SUPLEMENTAR DO ARTIGO PUBLICADO EM**  
*Frontiers in Ecology and Evolution* (Capítulo II)

***Supplementary Material***

**Butterfly assemblages from Amazonian flooded forests are not more species-poor than unflooded forests**

Rafael M. Rabelo<sup>1,2\*</sup>, Geanne C. N. Pereira<sup>2,3</sup>, João Valsecchi<sup>2</sup>, William E. Magnusson<sup>1,4</sup>

<sup>1</sup>Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil

<sup>2</sup>Grupo de Pesquisa em Ecologia de Vertebrados Terrestres, Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Amazonas, Brazil

<sup>3</sup>Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil

<sup>4</sup>Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil

**Corresponding author:** Rafael M. Rabelo (rmrabelo@gmail.com)

## Supplementary Figures and Tables

## Supplementary Figures

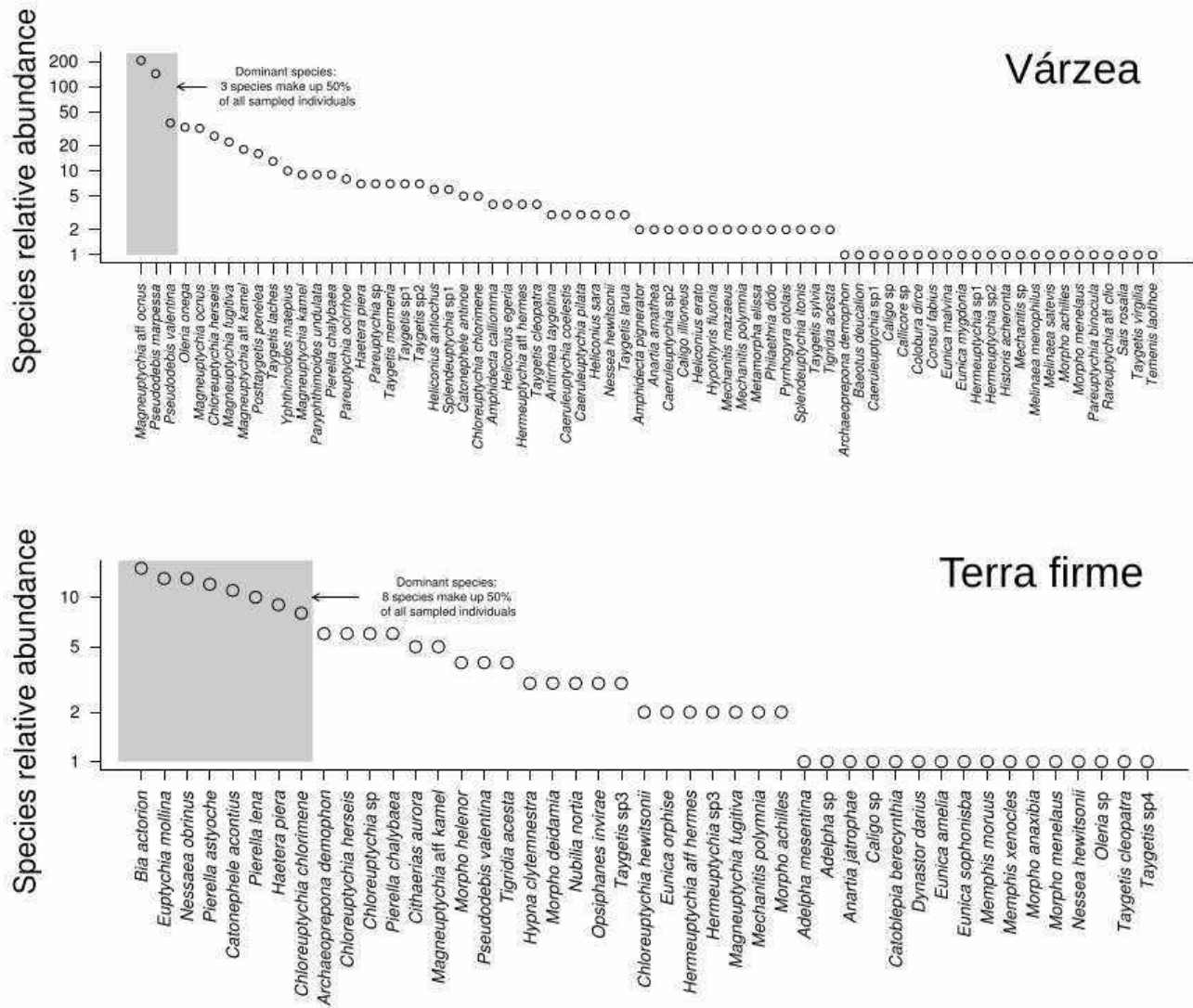
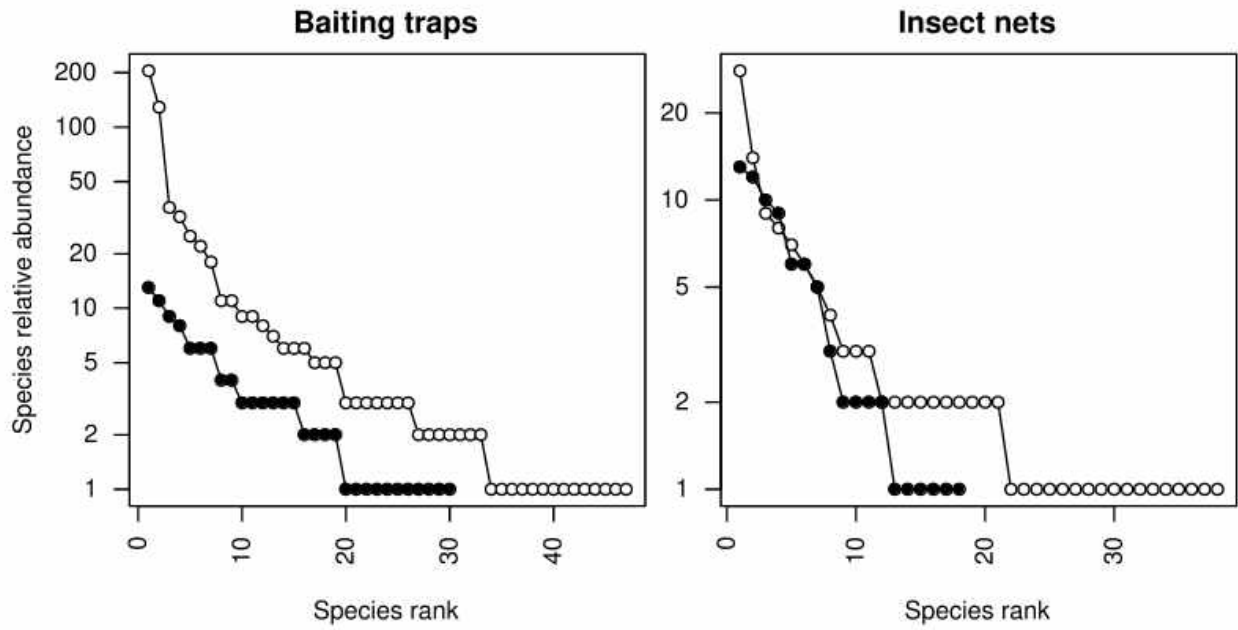
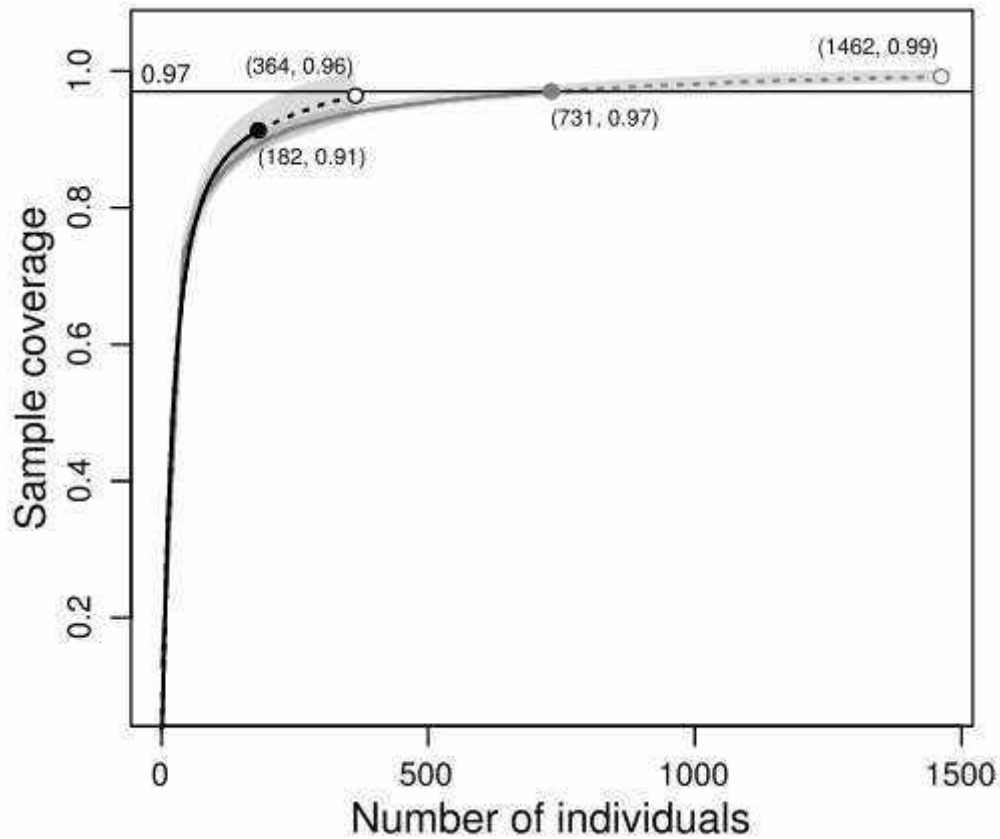


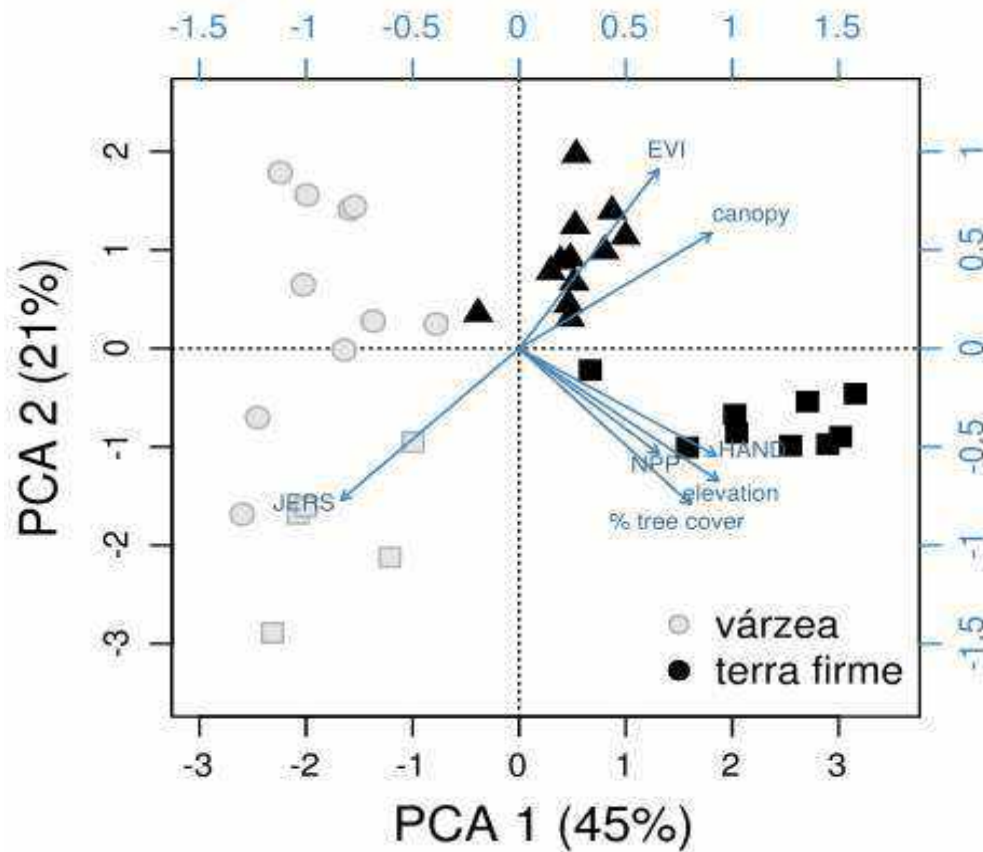
Figure S1. Rank-abundance distribution of butterfly species in várzea and terra firme forests.



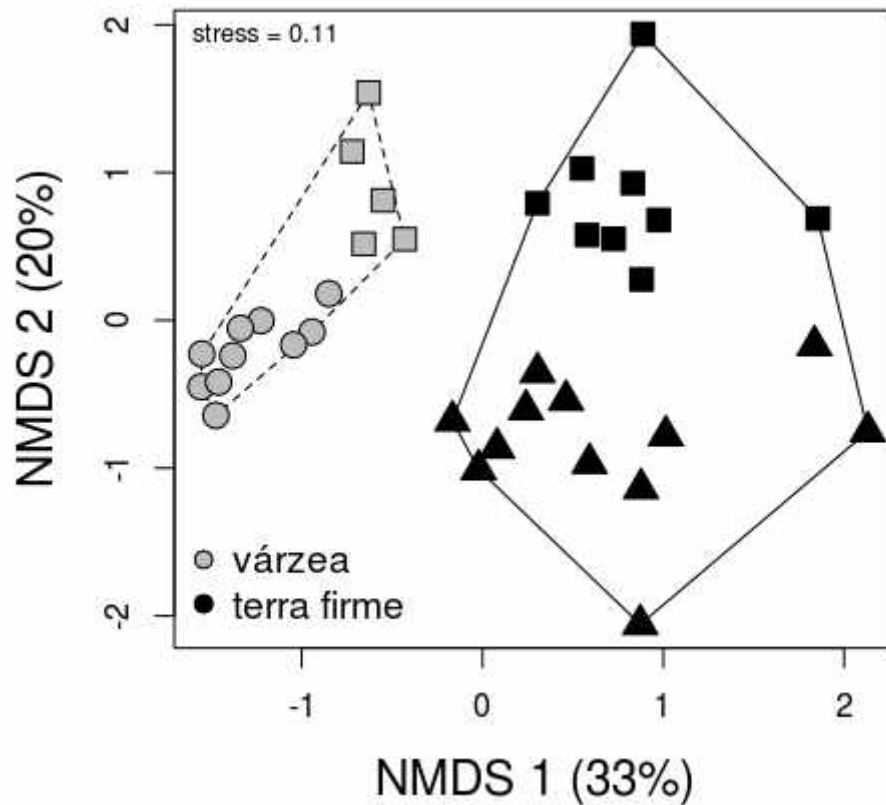
**Figure S2.** Species-abundance distribution of butterfly species in várzea and terra firme forests sampled with baited traps (left) and insect nets (right). In both sampling methods, the rank-abundance curves of species for different habitats came from different distributions (Kolmogorov-Smirnov, baited traps:  $D = 0.85$ ,  $p < 0.001$ ; insect nets:  $D = 0.71$ ,  $p < 0.001$ ).



**Figure S3.** Plot of sample coverage for rarefied samples (solid lines) and extrapolated samples (dashed lines) as a function of sample size for butterfly samples from *várzea* (gray lines) and *terra firme* (black lines) forests, with 95% confidence intervals (shaded areas). Observed samples are denoted by filled circles. Each of the two curves was extrapolated up to double its observed sample size. The numbers in parentheses are the sample size and the estimated sample coverage for each reference sample. Unfilled circles represent the number of individuals to be sampled from each assemblage when sample coverage is higher than 0.96 (i.e., the sample coverage at double the observed sample size for the *terra firme* assemblages).



**Figure S4.** Biplot of the first two axes from a PCA ordination of environmental variables across sampling plots. Distances between points represent the similarity between plots in terms of environmental variables. Square, circle and triangle symbols represent plots in Baixo Juruá, Mamirauá and Amanã reserves, respectively. Arrows show the correlation between axes and each variable, correlation coefficients is shown in blue axes. The first axis (PCA 1) clearly captured the differences in environmental variation across sampling plots and separate the *várzea* from *terra firme* plots. % tree cover – percent of tree cover in the landscape; canopy – canopy height; elevation – elevation above sea level; EVI – enhanced vegetation index; HAND – height above nearest drainage; JERS – terrain flooding; NPP – net primary productivity.



**Figure S5.** Difference in species composition between várzea and terra firme forests, excluding singletons and doubletons from community data. Each point in the graph represents a plot located in várzea or terra firme forest and the distance between points represents the similarity of plots in terms of their species composition, excluding singletons and doubletons. Square, circle and triangle symbols represent plots in Baixo Juruá, Mamirauá and Amanã reserves, respectively. Since our measure of species composition was based on abundance of each species, not presence-absence, individuals of rare species constituted a small proportion of individuals from the whole sampled community (6% várzea and 16% in terra firme). Therefore, the exclusion of singletons and doubletons from these analyses made very little difference in the pattern found. The butterfly composition from várzea forests were markedly different from the terra firme assemblages (PERMANOVA,  $F = 8.41$ ,  $p < 0.001$ ), and this difference was mainly captured by the first NMDS axis.

## Supplementary Tables

**Table S1.** Environmental variables and their correlation with first two axes derived from the PCA ordination.

| Type       | Variable  | PC1   | PC2   |
|------------|---|-------|-------|
| Topography | Elevation (SRTM) <sup>1</sup>                     | 0.87  | -0.34 |
|            | Height above nearest drainage (HAND) <sup>1</sup> | 0.84  | -0.09 |
|            | Terrain Flooding (JERS-1 SAR) <sup>2</sup>        | -0.67 | -0.54 |
| Vegetation | Canopy Height <sup>3</sup>                        | 0.81  | 0.17  |
|            | % Tree Cover <sup>4</sup>                         | 0.61  | -0.58 |
|            | Enhanced Vegetation Index (EVI) <sup>5</sup>      | 0.31  | 0.82  |
|            | Net Primary productivity (NPP) <sup>5</sup>       | 0.31  | -0.07 |

<sup>1</sup>DPI-INPE – Ambidata <<http://www.dpi.inpe.br/Ambidata/>>

<sup>2</sup>Synthetic Aperture Radar of the Japanese Earth Resources Satellite <<http://earth.esa.int>>

<sup>3</sup>Spatial Data Access Tool (SDAT) <<https://doi.org/10.3334/ORNLDAAAC/1388>>

<sup>4</sup>Global and Regional Risks of Tree Cover Loss <<http://futureclimates.conservation.org>>

<sup>5</sup>NASA Earth Observation <[neo.sci.gsfc.nasa.gov](http://neo.sci.gsfc.nasa.gov)>

**Table S2.** Abundance of Nymphalidae butterflies collected in 36 plots (15 in *várzea* and 21 in *terra firme* forests) in Baixo-Juruá Extractive Reserve, Mamirauá Sustainable Development Reserve and Amanã Sustainable Development Reserve, Amazonas State, Brazil.

| Species                        | <i>Várzea</i> | <i>Terra firme</i> |
|--------------------------------|---------------|--------------------|
| <b>DANAINAE</b>                |               |                    |
| Ithomiini                      |               |                    |
| <i>Hypothyris fluonia</i>      | 2             | 0                  |
| <i>Mechanitis mazaesus</i>     | 2             | 0                  |
| <i>Mechanitis polymnia</i>     | 2             | 2                  |
| <i>Mechanitis</i> sp.          | 1             | 0                  |
| <i>Melinaea menophilus</i>     | 1             | 0                  |
| <i>Melinaea satevis</i>        | 1             | 0                  |
| <i>Oleria onega</i>            | 33            | 0                  |
| <i>Oleria</i> sp.              | 0             | 1                  |
| <i>Sais rosalia</i>            | 1             | 0                  |
| <b>CHARAXINAE</b>              |               |                    |
| Anaeini                        |               |                    |
| <i>Consul fabius</i>           | 1             | 0                  |
| <i>Hypna clytemnestra</i>      | 0             | 3                  |
| <i>Memphis moruus</i>          | 0             | 1                  |
| <i>Memphis xenocles</i>        | 0             | 1                  |
| Preponini                      |               |                    |
| <i>Archaeoprepona demophon</i> | 1             | 6                  |
| <b>SATYRINAE</b>               |               |                    |
| Morphini                       |               |                    |
| <i>Antirrhea taygetina</i>     | 3             | 0                  |
| <i>Morpho achilles</i>         | 1             | 2                  |
| <i>Morpho anaxibia</i>         | 0             | 1                  |
| <i>Morpho deidamia</i>         | 0             | 3                  |
| <i>Morpho helenor</i>          | 0             | 4                  |
| <i>Morpho menelaus</i>         | 1             | 1                  |
| Brassolinii                    |               |                    |
| <i>Bia actorion</i>            | 0             | 15                 |
| <i>Caligo illioneus</i>        | 2             | 0                  |
| <i>Caligo</i> sp.              | 1             | 1                  |
| <i>Catoblepia berecynthia</i>  | 0             | 1                  |
| <i>Dynastor darius</i>         | 0             | 1                  |

|  |     |    |
|--|-----|----|
| <i>Opsiphanes invirae</i>              | 0   | 3  |
| Haeterini                              |     |    |
| <i>Cithaerias aurora</i>               | 0   | 5  |
| <i>Haetera piera</i>                   | 7   | 9  |
| <i>Pierella astyoche</i>               | 0   | 12 |
| <i>Pierella chalybaea</i>              | 9   | 6  |
| <i>Pierella lena</i>                   | 0   | 10 |
| Satyrini                               |     |    |
| <i>Amphidecta calliomma</i>            | 4   | 0  |
| <i>Amphidecta pignerator</i>           | 2   | 0  |
| <i>Caeruleptychia coelestis</i>        | 3   | 0  |
| <i>Caeruleptychia pilata</i>           | 3   | 0  |
| <i>Caeruleptychia</i> sp1.             | 1   | 0  |
| <i>Caeruleptychia</i> sp2.             | 2   | 0  |
| <i>Chloreptychia chlorimene</i>        | 5   | 8  |
| <i>Chloreptychia herseis</i>           | 26  | 6  |
| <i>Chloreptychia hewitsonii</i>        | 0   | 2  |
| <i>Chloreptychia</i> sp.               | 0   | 6  |
| <i>Euptychia mollina</i>               | 0   | 13 |
| <i>Hermeptychia</i> aff. <i>hermes</i> | 4   | 2  |
| <i>Hermeptychia</i> sp1.               | 1   | 0  |
| <i>Hermeptychia</i> sp2.               | 1   | 0  |
| <i>Hermeptychia</i> sp3.               | 0   | 2  |
| <i>Magneptychia</i> aff. <i>kamel</i>  | 18  | 5  |
| <i>Magneptychia</i> aff. <i>ocnus</i>  | 205 | 0  |
| <i>Magneptychia fugitiva</i>           | 22  | 2  |
| <i>Magneptychia kamel</i>              | 9   | 0  |
| <i>Magneptychia ocnus</i>              | 32  | 0  |
| <i>Nubilia nortia</i>                  | 0   | 3  |
| <i>Pareptychia binocula</i>            | 1   | 0  |
| <i>Pareptychia ocirrhoe</i>            | 8   | 0  |
| <i>Pareptychia</i> sp.                 | 7   | 0  |
| <i>Paryphthimoides undulata</i>        | 9   | 0  |
| <i>Posttaygetis penelea</i>            | 16  | 0  |
| <i>Pseudodebis marpessa</i>            | 143 | 0  |
| <i>Pseudodebis valentina</i>           | 37  | 4  |
| <i>Rareptychia</i> aff. <i>clio</i>    | 1   | 0  |

|                               |    |   |
|-------------------------------|----|---|
| <i>Splendeuphychia itonis</i> | 2  | 0 |
| <i>Splendeuphychia</i> sp.    | 6  | 0 |
| <i>Taygetis cleopatra</i>     | 4  | 1 |
| <i>Taygetis laches</i>        | 13 | 0 |
| <i>Taygetis larua</i>         | 3  | 0 |
| <i>Taygetis mermeria</i>      | 7  | 0 |
| <i>Taygetis sylvia</i>        | 2  | 0 |
| <i>Taygetis virgilia</i>      | 1  | 0 |
| <i>Taygetis</i> sp1.          | 7  | 0 |
| <i>Taygetis</i> sp2.          | 7  | 0 |
| <i>Taygetis</i> sp3.          | 0  | 3 |
| <i>Taygetis</i> sp4.          | 0  | 1 |
| <i>Ypthimoides maepius</i>    | 10 | 0 |

### HELICONIINAE

#### Heliconiini

|                             |   |   |
|-----------------------------|---|---|
| <i>Heliconius antiochus</i> | 6 | 0 |
| <i>Heliconius egeria</i>    | 4 | 0 |
| <i>Heliconius erato</i>     | 2 | 0 |
| <i>Heliconius sara</i>      | 3 | 0 |
| <i>Philaethria dido</i>     | 2 | 0 |

### LIMENITIDINAE

#### Limenitidini

|                          |   |   |
|--------------------------|---|---|
| <i>Adelpha mesentina</i> | 0 | 1 |
| <i>Adelpha</i> sp.       | 0 | 1 |

### BIBLIDINAE

#### Epicaliini

|                             |   |    |
|-----------------------------|---|----|
| <i>Catonephele acontius</i> | 0 | 11 |
| <i>Catonephele antioe</i>   | 5 | 0  |
| <i>Nessaia obrinus</i>      | 0 | 13 |
| <i>Nesaea hewitsonii</i>    | 3 | 1  |

#### Eunicini

|                          |   |   |
|--------------------------|---|---|
| <i>Eunica amelia</i>     | 0 | 1 |
| <i>Eunica malvina</i>    | 1 | 0 |
| <i>Eunica mygdonia</i>   | 1 | 0 |
| <i>Eunica orphise</i>    | 0 | 2 |
| <i>Eunica sophonisba</i> | 0 | 1 |

#### Epiphilini

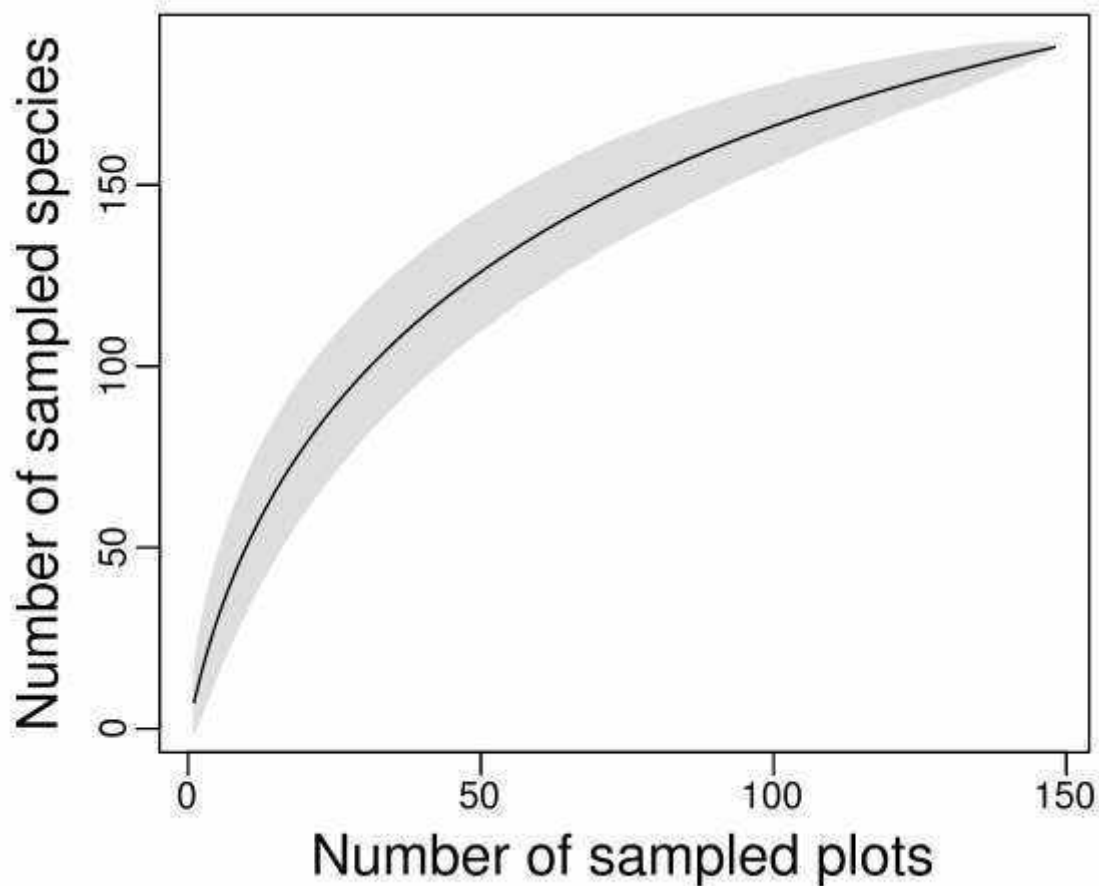
|                           |            |            |
|---------------------------|------------|------------|
| <i>Pyrrhogyra otolais</i> | 2          | 0          |
| <i>Temenis laothoe</i>    | 1          | 0          |
| Callicorini               |            |            |
| <i>Callicore</i> sp.      | 1          | 0          |
| <b>NYMPHALINAE</b>        |            |            |
| Coeini                    |            |            |
| <i>Baeotus deucalion</i>  | 1          | 0          |
| <i>Historis acheronta</i> | 1          | 0          |
| Nymphalini                |            |            |
| <i>Colobura dirce</i>     | 1          | 0          |
| <i>Tigridia acesta</i>    | 2          | 4          |
| Victoriniini              |            |            |
| <i>Anartia amathea</i>    | 2          | 0          |
| <i>Anartia jatrophae</i>  | 0          | 1          |
| <i>Metamorphia elissa</i> | 2          | 0          |
| <b>TOTAL</b>              | <b>731</b> | <b>182</b> |

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**APÊNDICE C - MATERIAL SUPLEMENTAR DO MANUSCRITO EM  
PREPARAÇÃO PARA *Ecography* (Capítulo III)**

**SUPPLEMENTARY MATERIAL**

Rabelo, R.M., Dambros, C., Graça, M.B.C.S., Pereira, G.C.N., Oliveira, I.F., Plaza, T.G.D., Valsecchi, J., Magnusson, W.E. 2021. The relative role of environment and dispersal as drivers of Amazonian fruit-feeding-butterfly distributions. - *Ecography* 000: 000-000.



**Figure S1.** Species accumulation curve. We found a high proportion (35%) of rare species (singletons and doubletons) so the species accumulation curve did not reach an asymptote.

**Table S1.** Pairwise correlation of predictor variables used in the raw-data-based approach. Correlation coefficients  $\geq |0.7|$  are shown in bold. longitude = decimal longitude; latitude = decimal latitude; |latitude| = module of decimal latitude (i.e., distance to the Equator); treecov = % of tree cover; canopy = canopy height; clay = soil clay content; sand = soil sand content; cation = soil cation concentration; annual\_temp = mean annual temperature; annual\_prec = annual precipitation; srad\_mean = mean annual solar radiation.

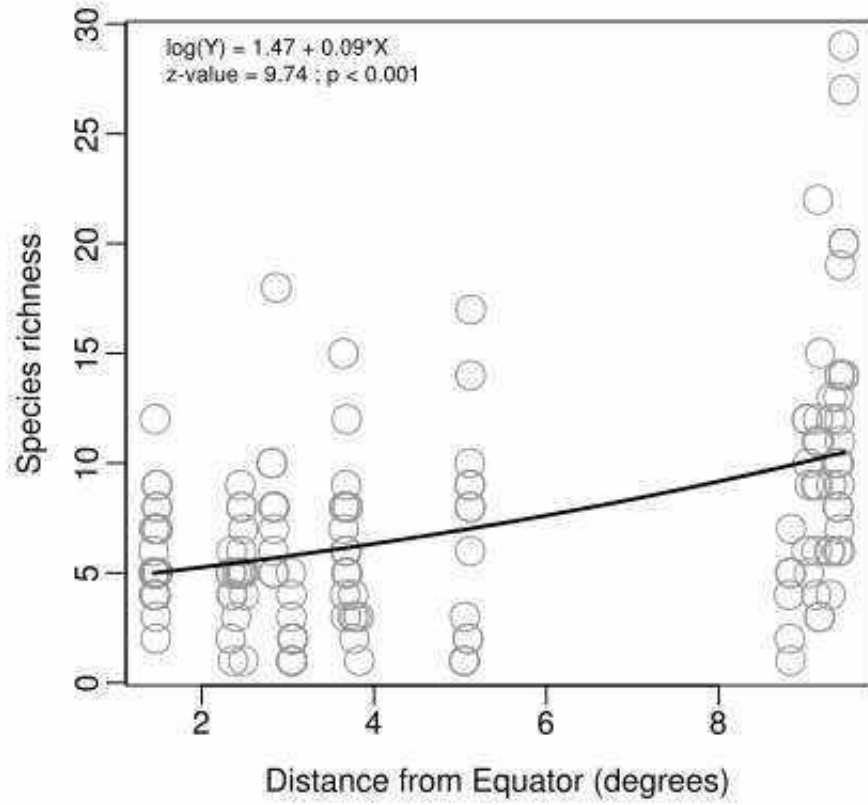
|             | longitude | latitude     | latitude | treecov | canopy | clay  | sand  | cation | annual_temp | annual_prec | srad_mean |
|-------------|-----------|--------------|----------|---------|--------|-------|-------|--------|-------------|-------------|-----------|
| longitude   | 1,00      |              |          |         |        |       |       |        |             |             |           |
| latitude    | 0,65      | 1,00         |          |         |        |       |       |        |             |             |           |
| latitude    | -0,55     | <b>-0,78</b> | 1,00     |         |        |       |       |        |             |             |           |
| treecov     | -0,20     | -0,30        | 0,47     | 1,00    |        |       |       |        |             |             |           |
| canopy      | -0,21     | -0,28        | 0,53     | 0,44    | 1,00   |       |       |        |             |             |           |
| clay        | 0,05      | -0,12        | 0,18     | 0,06    | 0,09   | 1,00  |       |        |             |             |           |
| sand        | 0,35      | 0,07         | 0,07     | 0,19    | 0,14   | -0,39 | 1,00  |        |             |             |           |
| cation      | -0,58     | -0,14        | 0,34     | 0,25    | 0,34   | -0,45 | 0,21  | 1,00   |             |             |           |
| annual_temp | -0,06     | -0,36        | -0,23    | -0,25   | -0,37  | -0,29 | 0,08  | -0,22  | 1,00        |             |           |
| annual_prec | -0,29     | -0,06        | -0,37    | -0,23   | -0,23  | 0,19  | -0,60 | -0,26  | 0,31        | 1,00        |           |
| srad_mean   | 0,65      | <b>0,88</b>  | -0,46    | -0,12   | -0,05  | -0,19 | 0,35  | 0,06   | -0,49       | -0,50       | 1,00      |

**Table S2.** Pairwise correlation of predictor variables used in the distance-based approach. Variables represent distance matrices quantifying the geographical distance, the degree of environmental difference, and the difference in area of endemism between pairs of sites. “geoDist” represents the geographical distance between pairs of sites. Environmental-distance matrices were calculated with Euclidean distances considering the whole set of environmental variables (envDist). Difference in the areas of endemism was defined as zero between plots in the same area of endemism area and one for plots in different areas.

|                | <b>geoDist</b> | <b>envDist</b> | <b>AoEDist</b> |
|----------------|----------------|----------------|----------------|
| <b>geoDist</b> | 1,00           |                |                |
| <b>envDist</b> | 0,59           | 1,00           |                |
| <b>AoEDist</b> | 0,54           | 0,29           | 1,00           |

**Table S3.** Ranking of models with different combinations of predictor variables for explaining species richness according to AICc. Table shows only models with delta AICc < 4. prec = annual precipitation; temp = mean annual temperature; canopy = canopy height; cation = log(soil cation concentration); clay = soil clay content; lat = module of latitude (i.e., distance to Equator); long = longitude; sand = soil sand content; treecov = % of tree cover. Minus signs (-) indicates variables not selected in the model.

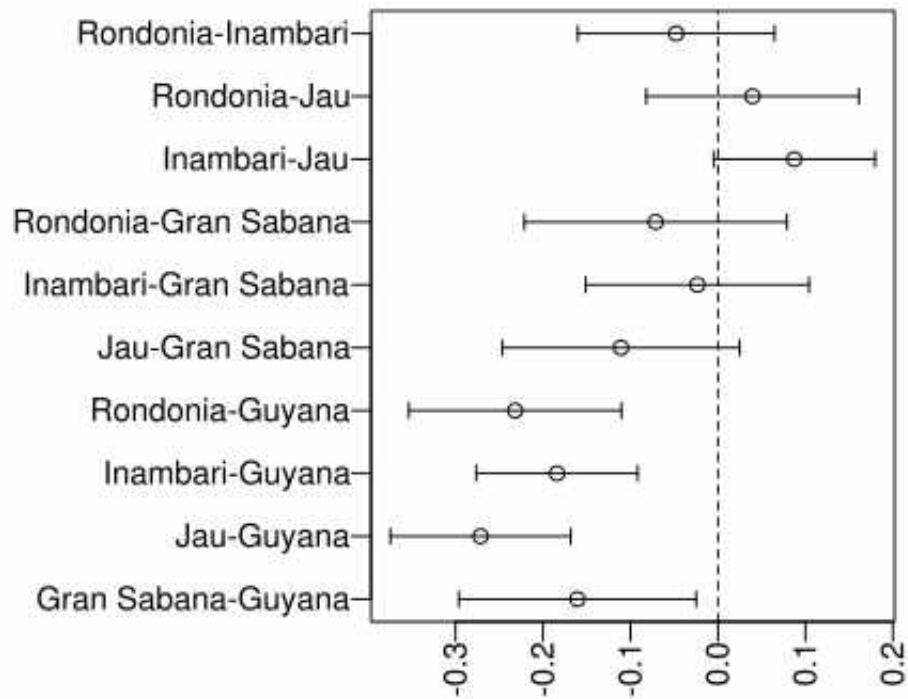
| Intercept | prec  | temp | canopy | cation | clay  | lat   | long  | sand  | treecov | R <sup>2</sup> | df | logLik  | AICc   | delta | weight |
|-----------|-------|------|--------|--------|-------|-------|-------|-------|---------|----------------|----|---------|--------|-------|--------|
| 1.92      | -0.33 | NA   | 0.13   | -0.29  | -0.08 | -0.01 | -0.46 | NA    | -0.13   | 0.58           | 8  | -423.21 | 863.45 | 0.00  | 0.38   |
| 1.92      | -0.35 | NA   | 0.14   | -0.30  | -0.09 | -0.02 | -0.46 | -0.04 | -0.13   | 0.58           | 9  | -422.96 | 865.22 | 1.77  | 0.16   |
| 1.93      | -0.33 | NA   | 0.12   | -0.24  | NA    | -0.02 | -0.44 | NA    | -0.13   | 0.57           | 7  | -425.35 | 865.51 | 2.05  | 0.13   |
| 1.92      | -0.34 | 0.01 | 0.14   | -0.29  | -0.07 | 0.00  | -0.47 | NA    | -0.13   | 0.58           | 9  | -423.19 | 865.68 | 2.23  | 0.12   |
| 1.92      | -0.36 | 0.07 | 0.15   | -0.27  | NA    | 0.04  | -0.49 | NA    | -0.12   | 0.58           | 8  | -424.48 | 865.99 | 2.54  | 0.11   |
| 1.92      | -0.36 | 0.03 | 0.15   | -0.31  | -0.09 | 0.01  | -0.48 | -0.04 | -0.12   | 0.58           | 10 | -422.87 | 867.36 | 3.90  | 0.05   |
| 1.93      | -0.32 | NA   | 0.12   | -0.24  | NA    | -0.01 | -0.44 | 0.02  | -0.13   | 0.57           | 8  | -425.21 | 867.45 | 4.00  | 0.05   |



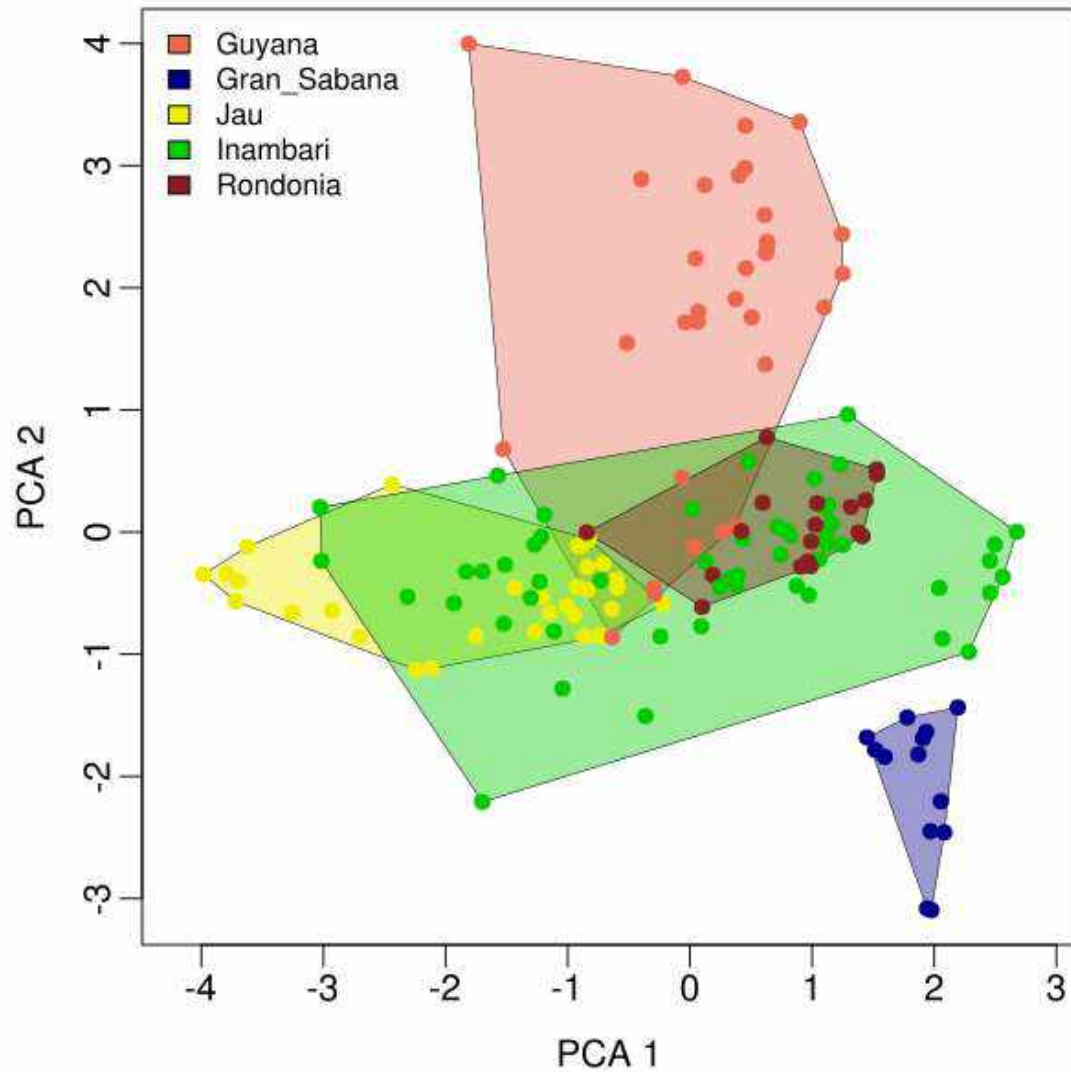
**Figure S2.** Variation of species richness (y-axis) according to distance from Equator, in degrees (x-axis). Gray circles represent each sampled plot and black line represent the change in the mean species richness with increasing distance from Equator according to a Poisson regression model.

**Table S4.** Ranking of models with different combinations of predictor variables for explaining species composition according to AICc. Table shows only models with delta AICc < 4. prec = annual precipitation; temp = mean annual temperature; AoE = area of endemism (categorical factor); canopy = canopy height; cation = log(soil cation concentration; clay = soil clay content; lat = module of latitude (i.e., distance to Equator); long = longitude; sand = soil sand content; treecov = % of tree cover. Plus signs (+) indicates that the variable include in the model (coefficients not presented because is categorical (region); minus signs (-) indicates variables not selected in the model.

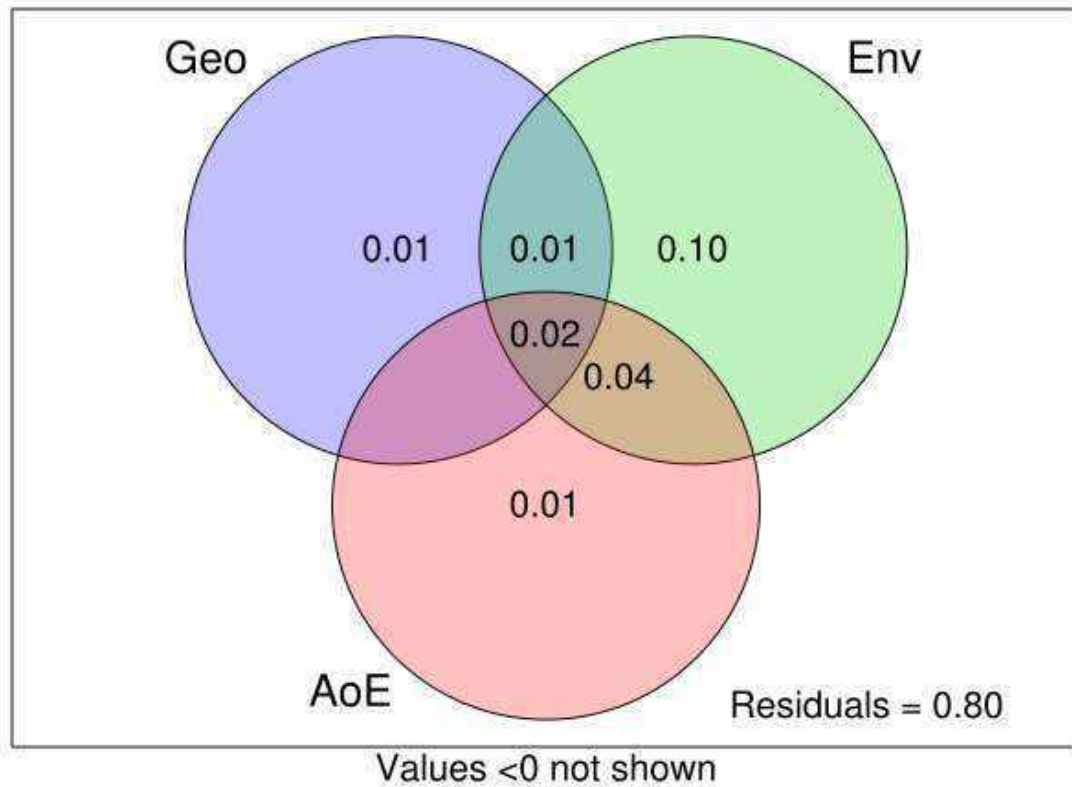
| (Intercept) | prec  | temp  | AoE | canopy | cation | clay  | latitude | longitude | sand  | tree.cov | R <sup>2</sup> | df | logLik | AICc    | delta | weight |
|-------------|-------|-------|-----|--------|--------|-------|----------|-----------|-------|----------|----------------|----|--------|---------|-------|--------|
| 0.38        | -0.12 | -0.07 | +   | -      | -0.08  | -     | 0.01     | -0.13     | -0.11 | -0.02    | 0.48           | 13 | 96.75  | -164.79 | 0.00  | 0.17   |
| 0.40        | -0.12 | -0.07 | +   | -      | -0.09  | -     | 0.01     | -0.14     | -0.12 | -        | 0.47           | 12 | 95.51  | -164.72 | 0.07  | 0.16   |
| 0.38        | -0.10 | -     | +   | -      | -0.08  | -     | -0.01    | -0.14     | -0.11 | -        | 0.46           | 11 | 94.24  | -164.55 | 0.24  | 0.15   |
| 0.36        | -0.09 | -     | +   | -      | -0.07  | -     | -0.02    | -0.13     | -0.10 | -0.02    | 0.47           | 12 | 95.34  | -164.37 | 0.41  | 0.14   |
| 0.38        | -0.11 | -0.07 | +   | -      | -0.08  | -0.01 | 0.00     | -0.13     | -0.11 | -0.02    | 0.48           | 14 | 96.81  | -162.47 | 2.31  | 0.05   |
| 0.40        | -0.12 | -0.07 | +   | -      | -0.09  | -0.01 | 0.01     | -0.13     | -0.12 | -        | 0.47           | 13 | 95.58  | -162.44 | 2.35  | 0.05   |
| 0.38        | -0.10 | -     | +   | -      | -0.08  | -0.01 | -0.02    | -0.13     | -0.11 | -        | 0.46           | 12 | 94.36  | -162.41 | 2.38  | 0.05   |
| 0.38        | -0.12 | -0.08 | +   | 0.00   | -0.09  | -     | 0.01     | -0.13     | -0.11 | -0.02    | 0.48           | 14 | 96.78  | -162.41 | 2.38  | 0.05   |
| 0.40        | -0.12 | -0.07 | +   | 0.00   | -0.09  | -     | 0.02     | -0.14     | -0.12 | -        | 0.47           | 13 | 95.53  | -162.33 | 2.45  | 0.05   |
| 0.36        | -0.09 | -     | +   | -      | -0.08  | -0.01 | -0.03    | -0.13     | -0.10 | -0.02    | 0.47           | 13 | 95.46  | -162.21 | 2.58  | 0.05   |
| 0.37        | -0.10 | -     | +   | 0.00   | -0.08  | -     | -0.01    | -0.13     | -0.11 | -        | 0.46           | 12 | 94.25  | -162.19 | 2.60  | 0.05   |
| 0.36        | -0.09 | -     | +   | 0.00   | -0.07  | -     | -0.02    | -0.13     | -0.10 | -0.02    | 0.47           | 13 | 95.34  | -161.97 | 2.82  | 0.04   |



**Figure S3.** Differences in butterfly community composition among areas of endemism in Amazonia. Coefficients shown in the x-axis were estimated as the mean difference between values of the first PCoA axis, which represents species composition in each sampling plot. Circles and horizontal lines represent the means and confidence intervals of the difference in species composition between pairs of areas of endemism.



**Figure S4.** Ordination plot according to a Principal Component Analysis (PCA) to summarize environmental conditions among areas of endemism. Distance between points represent their similarity between plots according to their environmental conditions. Point colors represent the major bird areas of endemism, and polygons overlap may be interpreted as the degree of environmental similarity among areas of endemism.



**Figure S5.** Venn diagram showing the relative contribution ( $R^2$ ) of geographical distance (Geo); environmental distance (Env) and differences in areas of endemism (AoE) to explain butterfly compositional similarity in Amazonia. Compositional similarity was measured by 1-Jaccard index between pairs of sites. Relative contributions were determined using multiple regressions on distance matrices and variance partitioning. Values show the amount of variance that was uniquely or jointly explained by the components. Components with  $R^2 < 0$  are not shown.